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# A MORPHOLOGICAL STUDY OF FLOWER AND SEED DEVELOPMENT IN PEPPER[1]

By H. L. COCHRAN[2]

*Associate horticulturist, Georgia Agricultural Experiment Station*

## INTRODUCTION

Of the many economically important vegetable crop plants, few have been more neglected from the standpoint of type improvement than the pepper (*Capsicum frutescens* L.). Many of the common varieties are lacking in uniformity of fruit shape, in thickness of flesh, in smallness of placenta, and in color. Most varieties are also susceptible to certain destructive diseases, some of which could be controlled by the use of scientific methods of breeding and selection in producing resistant strains. Before any improvement program is undertaken through breeding methods, however, the morphology of the flower should be better understood. A knowledge of the method and time of pollination, the time required for fertilization, and the behavior of the flower throughout its development are also important.

## MATERIALS AND METHODS

The World Beater variety of pepper was used exclusively for this study. Some of the plants from which material was collected were grown in the experimental greenhouses of the Department of Vegetable Crops of the New York State College of Agriculture at Ithaca, N. Y., during the fall and winter of 1932–33; others were grown in the horticultural greenhouses of the Georgia Experiment Station at Experiment, Ga., during the winter of 1935–36. The material for study was killed and fixed in a solution made up of solution A, consisting of 4 parts of commercial 40 percent formalin and 1 part of water, and solution B, consisting of 1 g of chromic acid and 10 cc of acetic acid in 90 cc of water. Equal parts of these two solutions were mixed at the time they were used. The material was then dehydrated in alcohol and embedded in paraffin, xylol being used according to the usual laboratory method. Both transverse and longitudinal sections were cut, 10$\mu$ to 12$\mu$ in thickness, mounted serially, and stained in Heidenhains' iron-alum haematoxylin. All figures were drawn with the aid of a camera lucida.

## DEVELOPMENT OF THE FLOWER

Small (*21, p. 992*)[3] describes the pepper flower as being solitary in the axils or in small cymes. The calyx is barely accrescent and has five wholly or partly united sepals. The corolla is usually white,

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[3] Reference is made by number (italic) to Literature Cited, p. 418.

nearly rotate, five-lobed, and imbricated. There are typically five stamens adnate to the base of the corolla. The anthers are bluish and dehisce by longitudinal splitting. The stigma is club-shaped or dilated.

The time of flower primordia differentiation in the pepper was found by Auchter and Harley (*1*) to be influenced to some extent by photoperiod. More recently Cochran (*7*) found that temperature, as well as photoperiod, was of great importance. The protuberance of the first or terminal flower of the cyme arises in the axil of a leaf and in some cases of a branch. The two succeeding flowers of the cyme each

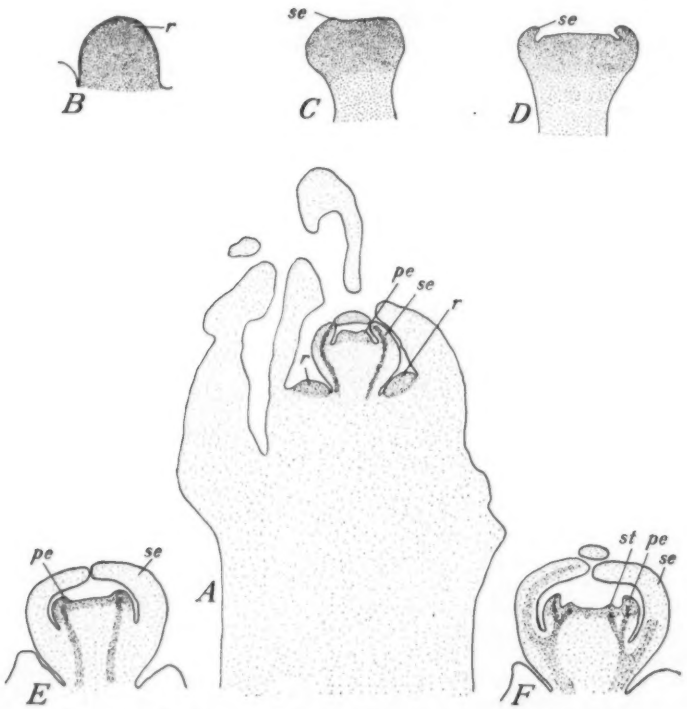



FIGURE 1.—*A*, Longitudinal section of developing flower of cyme. *B*, *C*, *D*, Meristematic region of receptacles: *B*, no floral organs differentiated; *C*, *D*, sepals differentiating. *E*, Early development of petals. *F*, Sepals, petals, and stamens developing. *r*, receptacle; *se*, sepals; *pe*, petals; *st*, stamens. All × 225.

arise from similar protuberances which have grown out from the base of the pedicel of the preceding flower (fig. 1, *A*). The growing apex or protuberance is at first somewhat conical (fig. 1, *B*), but subsequently becomes flattened and broadened (fig. 1, *C*). The primordia of the first floral organs arise on the periphery of the flattened meristematic protuberance, indicating the beginning of the sepal lobes (fig. 1, *C*, *D*). These rudimentary sepals curve inward, arching over the apex of the axis. Primordia of the second whorl soon appear in the same manner but are slightly higher on the axis and are alternate with the sepal lobes. These give rise to the petals (fig. 1, *E*). Subsequently

there appears on the axis and nearer the center, opposite the sepal lobes and alternate with the petals, a third set of small protuberances

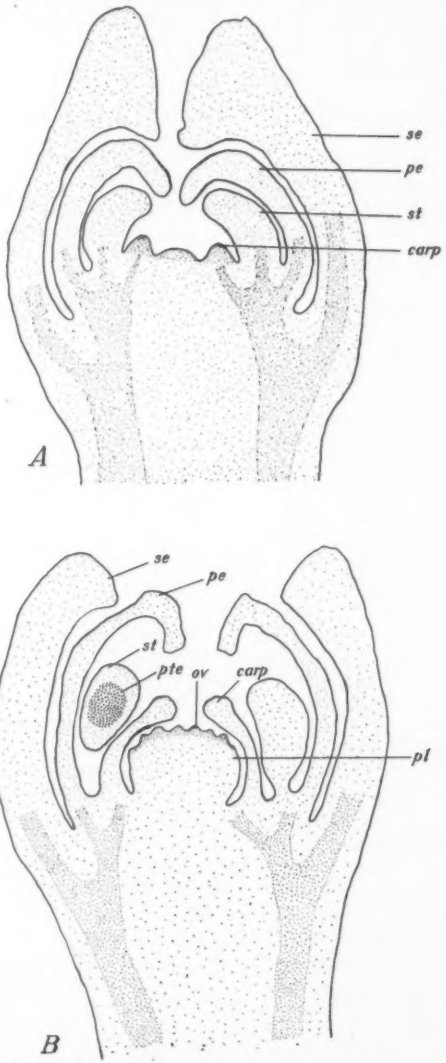



FIGURE 2.—*A*, Initiation of carpels and development of sepals, petals, and stamens, × 225; *B*, longitudinal section of young flower showing further development of sepals, petals, stamens, and carpels; young ovules in macrospore mother-cell stage and microspores in tetrad stage, × 440; *se*, sepals; *pe*, petals; *st*, stamens; *carp*, carpels; *pte*, pollen tetrads; *ov*, ovules; *pl*, placenta.

which develop into the stamens (fig. 1, *F*). The carpels are the last cycle of flower organs to differentiate. They arise from the center of

the floral axis and develop into a compound pistil consisting usually of three united carpels (fig. 2, *A*, *B*). A pepper flower in transverse section is shown in figure 4, *A*. The petals and stamens curve inward over the top of the carpels. These observations are in complete agreement with those of Béla (*2*) for the pepper and with Cooper (*10*) and Smith (*23*) for the tomato.

## MACROSPOROGENESIS AND DEVELOPMENT OF THE MACROGAMETOPHYTE

The young ovules are first distinguishable as small, rapidly growing protuberances which arise from the placental tissue (fig. 2, *B*; fig. 3, *A*, *B*, *C*). Occasionally internal abnormalities, the description and morphology of which have been described by Cochran (*8*), arise simultaneously with the young ovules and for a while cannot be distinguished from the normal ovules. The ovules soon become somewhat pointed (fig. 5, *A*) as the result of more rapid cell division on one side of the ovule than on the other, but eventually they become anatropous in form. This type of ovule is the commonest among the modern flowering plants, and has been found by Chatin (*6*), Cooper (*11*), Bhaduri (*3*), and Smith (*23*) to be typical for various other members of the Solanaceae. When the developing ovule has attained the stage shown in figure 4, *C*, the hypodermal archesporial cell, which functions as the macrospore mother cell in pepper, has already become differentiated in the nucellus. This occurs a little before the initiation of the integument. The archesporial cell is distinguishable on account of its large size, its conspicuous nucleus, and heavily stained cytoplasm. The macrospore mother cell becomes several times larger than the hypodermal archesporial cell from which it arises and is enclosed by a single-layered nucellus on the sides and apex (fig. 5, *B*).

The primordium of the integument is not evident until after the differentiation of the archesporial cell. The integument arises as an outgrowth from the base of the nucellar tissue and continues to develop until it finally surrounds the nucellus and elongates so as to form a micropyle some 8 to 10 cells in length (fig. 5, *B*, *C*; fig. 6, *A*). Further growth of the nucellus occurs by anticlinal division of the cells. The nucellus consists of a single layer of cells and is thought to nourish the nascent embryo. It completely degenerates as the embryo sac develops.

The much enlarged macrospore mother cell, by two successive divisions, gives rise to a linear row of four macrospores of approximately the same size (fig. 5, *B*, *C*; fig. 6, *A*). The three macrospores nearest the micropyle soon degenerate, leaving the macrospore at the chalazal end to function as the one-celled embryo sac (fig. 6, *B*, *C*). Before the first division of its nucleus the functioning macrospore increases rapidly in size. Simultaneously with this rapid growth, however, the cells of the nucellus gradually become disorganized and finally disappear (fig. 7, *A*, *B*, *C*). The work of Young (*28*) shows that the nucellus cells in the potato fail to degenerate. In a more recent study of macrosporogenesis and development of the macrogametophyte in the potato, however, Rees-Leonard (*19*) has shown that cells of the nucellus disappear in practically the same manner as described in this study for pepper.

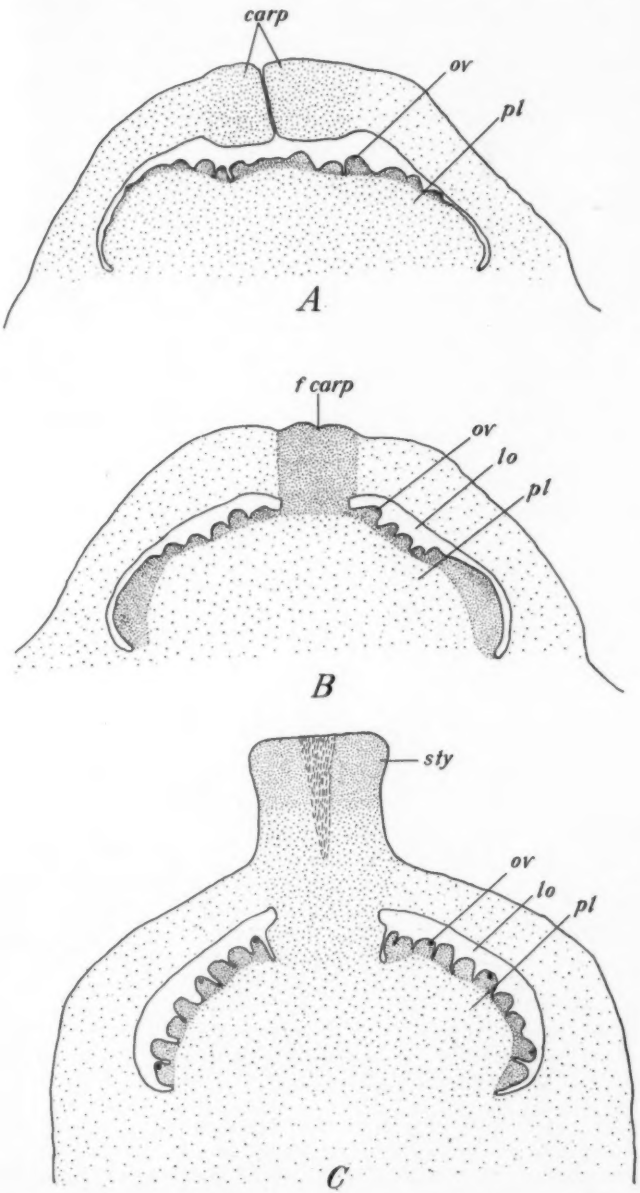



FIGURE 3.—*A*, Carpels just prior to fusing; developing ovules. *B*, Carpels fused, setting off two loculi; style development started. *C*, Style development complete; ovules further developed. *carp*, carpels; *ov*, ovules; *pl*, placenta; *f carp*, fused carpels; *lo*, loculus; *sty*, style. All × 440.

The first gametophytic division occurs in the central portion of the embryo sac (fig. 6, *C;* fig. 7, *A*). The resulting daughter nuclei separate, one migrating toward the mocropylar end and the other toward the chalazal end of the embryo sac (fig. 7, *B*). By two subsequent successive divisions, the two daughter nuclei produce eight

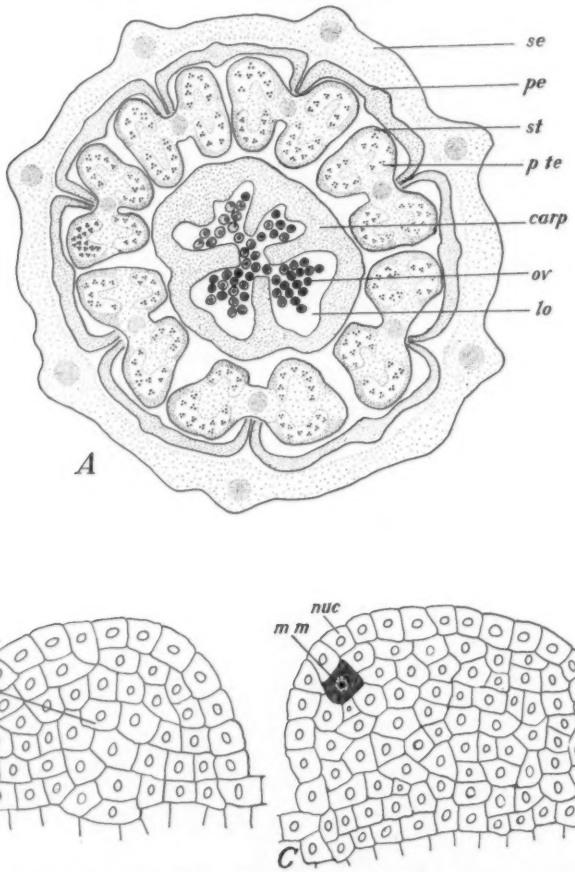



FIGURE 4.—*A*, Transverse section of pepper flower at the macrospore mother-cell and microspore tetrad stages; same stage as shown in figure 2, *B*. Note presence of seven stamens; five is the usual number. × 440. *B*, Young ovule soon after having arisen from placental tissue. × 950. *C*, Developing ovule with macrospore mother cell. × 950. *se*, Sepals; *pe*, petals; *st*, stamens; *p te* pollen tetrads; *carp*, carpels; *ov*, ovule; *lo*, loculus; *m m*, macrospore mother cell; *nuc*, nucellus.

nuclei. Two of the eight nuclei take a position near the center of the sac and become the polar nuclei; three migrate to the chalazal end of the sac and become the antipodals; and the three remaining nuclei take a position near the micropylar end of the sac. Of these the two more pear-shaped ones become the synergids, and the rather spherical one the egg (fig. 7, *D*). Guignard (*15*) as early as 1882 studied the development of the female gametophyte in some solanaceous plants,

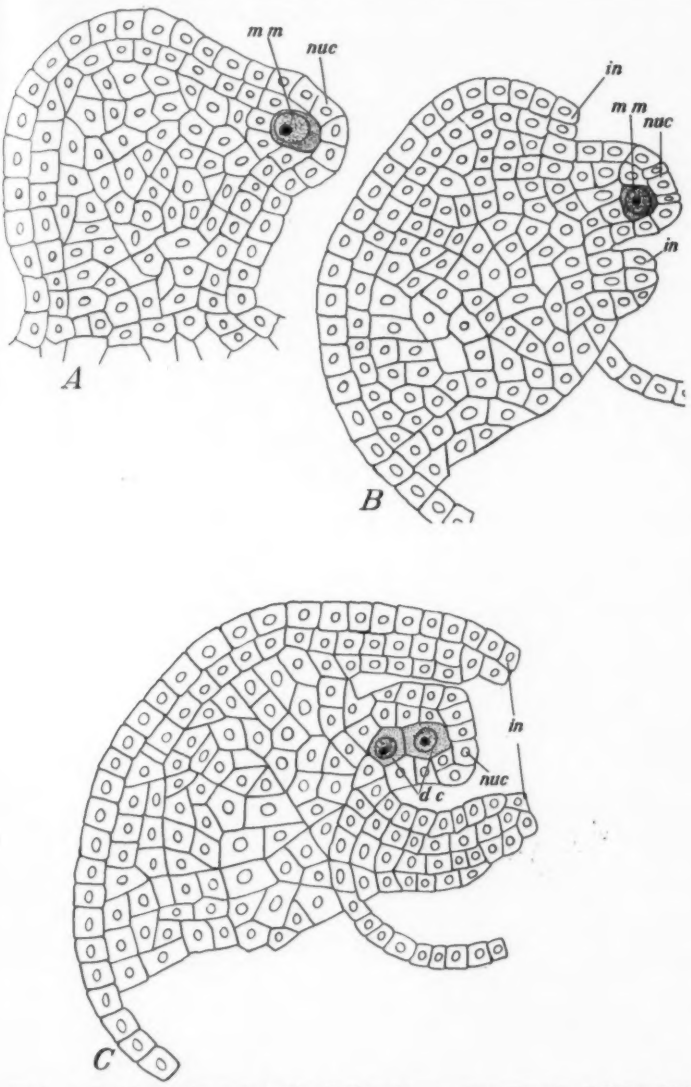



FIGURE 5.—*A, B, C,* Developing ovule showing divisions of macrospore mother cell. Initation of integument shown in *B, C* shows further growth of integument and two daughter nuclei as a result of the first division of the macrospore mother cell. *m m,* Macrospore mother cell; *nuc,* nucellus; *in,* integument; *d c,* daughter cells. All × 950.

among which were included *Nicotiana tabacum* and *Cestrum splendens.* He concluded that the development of the embryo sac in these plants follows the normal type or the same as that reported here. Banerji,[4] working with *Capsicum annuum,* and Cooper (*11*) and Smith (*23*),

[4] BANERJI, E. A. CYTOLOGY OF CAPSICUM. Unpublished thesis, Univ. Calif. 1931.

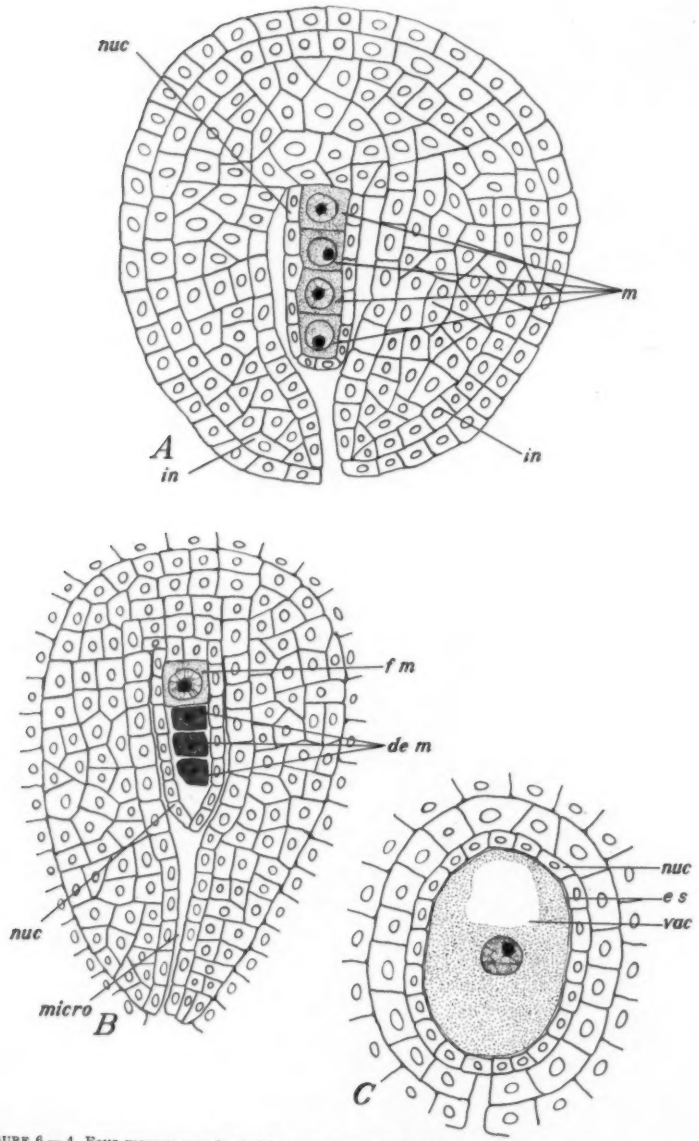



FIGURE 6.—*A*, Four macrospores formed by two successive divisions of the macrospore mother cell. *B*, Tetrad of macrospores, showing the functioning and three degenerating macrospores. *C*, one-nucleate embryo sac. *nuc*, Nucellus; *m* macrospores; *in*, integument; *f m*, functioning megospore; *de m*, degenerating macrospore; *e s*, embryo sac; *vac*, vacuole; *micro*, micropyle. All × 950.

with *Lycopersicon esculentum*, found the same type of development of the embryo sac. Soon after the development of the mature or eight-nucleate embryo sac, the antipodal cells begin to degenerate,

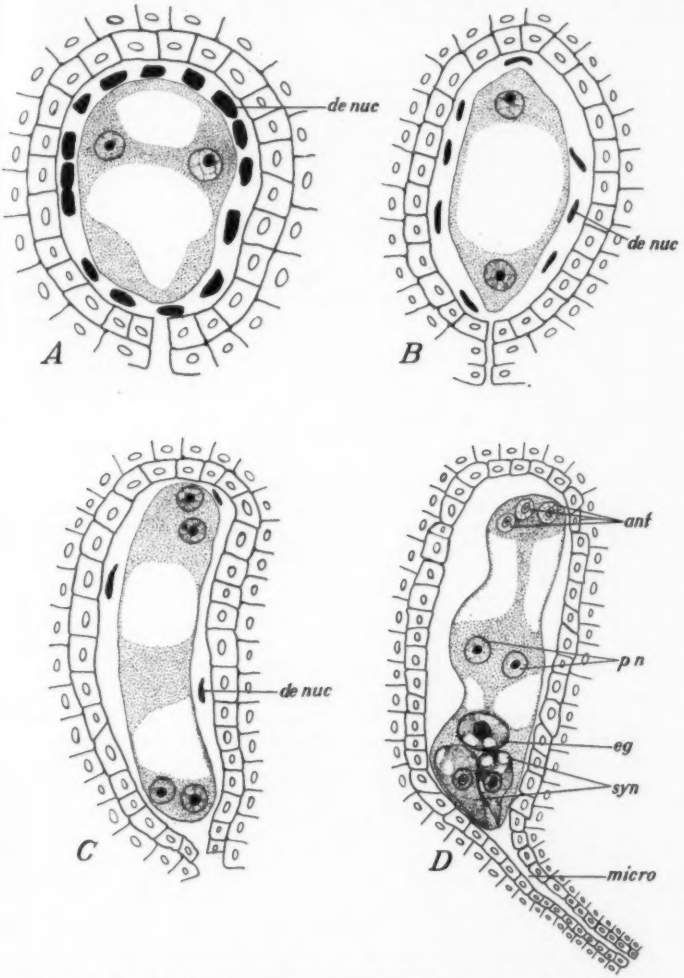



FIGURE 7.—*A*, *B*, Two-nucleate embryo sac; nucellus beginning to degenerate. *C*, Four-nucleate embryo sac; nucellus practically gone. *D*, Eight-nucleate or mature embryo sac. *de nuc*, Degenerating nucellus; *ant*, antipodal nuclei; *p n*, polar nuclei; *eg*, egg; *syn*, synergids; *micro*, micropyle. All × 640.

and by the time fertilization has taken place, only distorted portions of them remain. Fusion of the polar nuclei takes place just before or at the time of fertilization.

## MICROSPOROGENESIS AND DEVELOPMENT OF THE MICROGAMETOPHYTE

Prior to any archesporial differentiation, the anthers consist of a homogeneous mass of meristematic tissue (fig. 8, *B*). However, when the young stamens have reached the stage of development shown in figure 2, *A*, a single row of hypodermal archesporial cells can be seen. These cells are easily distinguished by their deeply stained contents and large nuclei. The archesporial cells (fig. 8, *C*) first divide periclinally (fig. 8, *D*), thus giving rise to a single row of pollen mother cells on the inside and an outer layer of similar cells which divide to form the tapetum, the middle layer, and the endothecium (fig. 8, *E*). The tapetal cells are at first uninucleate, but subsequently divide and become binucleate (fig. 9, *A*). Soon after the sporogenous cells begin to separate and round off, the cells of the tapetum begin to enlarge and change their original shape (fig. 9, *B*, *C*). The cells are not long; some enlarge tangentially as well as radially and appear somewhat square, while others are irregular in shape. At the time of the late anaphase of the first meiotic division of the pollen mother cells, the tapetal cells show signs of degeneration. As they grow older they gradually lose their contents which are supposedly absorbed by the developing pollen. They are quite distorted by the time the pollen tetrad stage is reached and subsequently collapse entirely.

The first signs of degeneration of the middle layer are noted during the metaphase of the first meiotic division. These cells seem to degenerate in the beginning at a faster rate than do the tapetal cells, although they are not entirely absorbed even at the time of pollen tetrad formation. Cells of the endothecium do not undergo the above-described change.

In figure 9, *D*, is shown the pollen mother cells in the telophase of the second meiotic division with cell walls just beginning to form. At this time the macrogametophyte has started to enlarge, and is in the macrospore mother-cell stage of development. Tetrads rounded off and enclosed within the pollen mother cell wall are to be seen in figure 10, *A*. At the time they are set free from the enclosure, the walls of the microspores are very thin, but later they become considerably thickened (fig. 10, *B*, *C*). The microspore nucleus, which contains the reduced number of chromosomes, divides to two, around one of which a membrane cuts out a generative cell. The other nucleus develops into the vegetative or tube cell, which later grows out to form the pollen tube. The generative cell divides to form two male gametes within the growing pollen tube before the latter reaches the embryo sac. Mature microgametophytes are to be seen in figure 10, *C*. Many microspores develop within the loculi of each anther.

## ANTHESIS

A close study of anthesis and fruit setting in *Capsicum frutescens* was made by the writer under both greenhouse and field conditions at Ithaca, N. Y., over a 4-year period. Factors considered in this work included temperature, soil moisture, soil nitrogen content, atmospheric humidity, and photoperiod. The first- and last-named factors proved to have the greatest influence on anthesis.

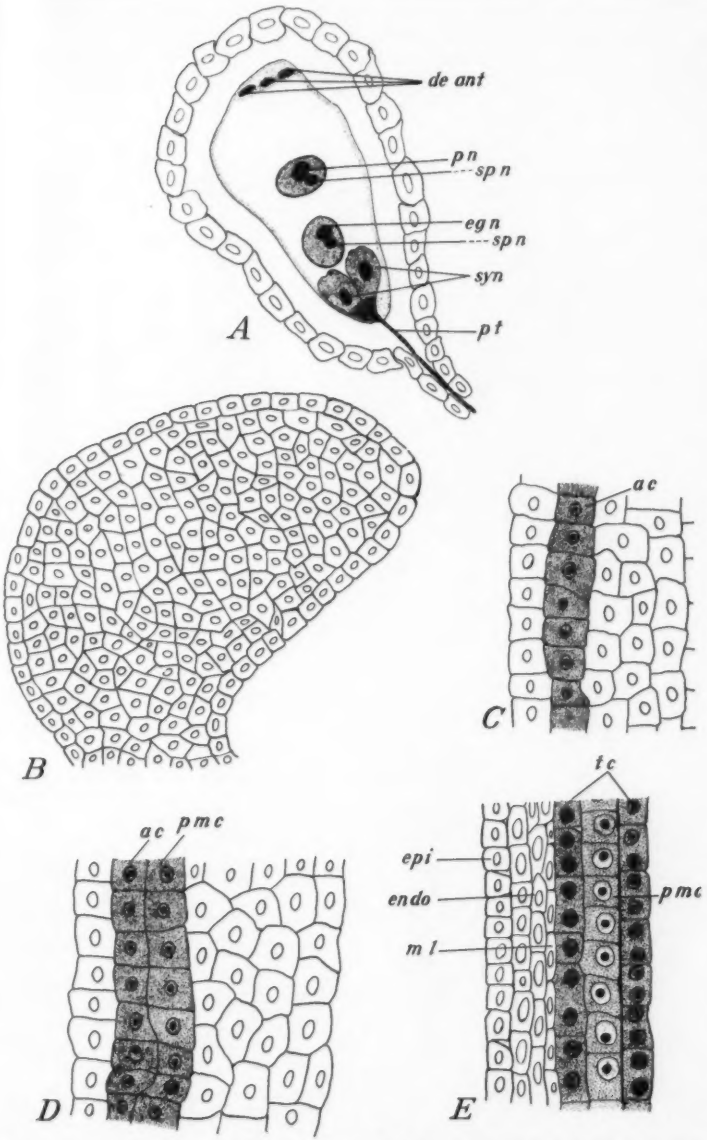



FIGURE 8.—*A*, Fertilization 42 hours after pollination; antipodals degenerating; triple fusion of two polar nuclei with sperm nucleus; egg nucleus fused with other sperm nucleus. × 950. *B*, Longitudinal section of young anther prior to differentiation of archesporial cells. × 225. *C*, Row of archesporial cells in anther. × 640. *D*, Archesporial cells divided, cutting off row of pollen mother cells on inside. × 640. *E*, Row of pollen mother cells enclosed by two rows of two-nucleate tapetal cells. × 640. *de ant*, Degenerating antipodals; *p n*, polar nuclei; *sp n*, sperm nucleus; *eg n*, egg nucleus; *syn*, synergids; *p t*, pollen tube; *a c*, archesporial cells; *p m c*, pollen mother cells; *epi*, epidermis; *endo*, endothecium; *m l*, middle layer; *t c*, tapetal cells.

Plants in the greenhouse were grown from seed to maturity under four different temperatures, namely, 50° to 60°, 60° to 70°, 70° to 80°, and 90° to 100° F. All other conditions were kept as nearly optimum for growth as possible. Long and normal day conditions were main-

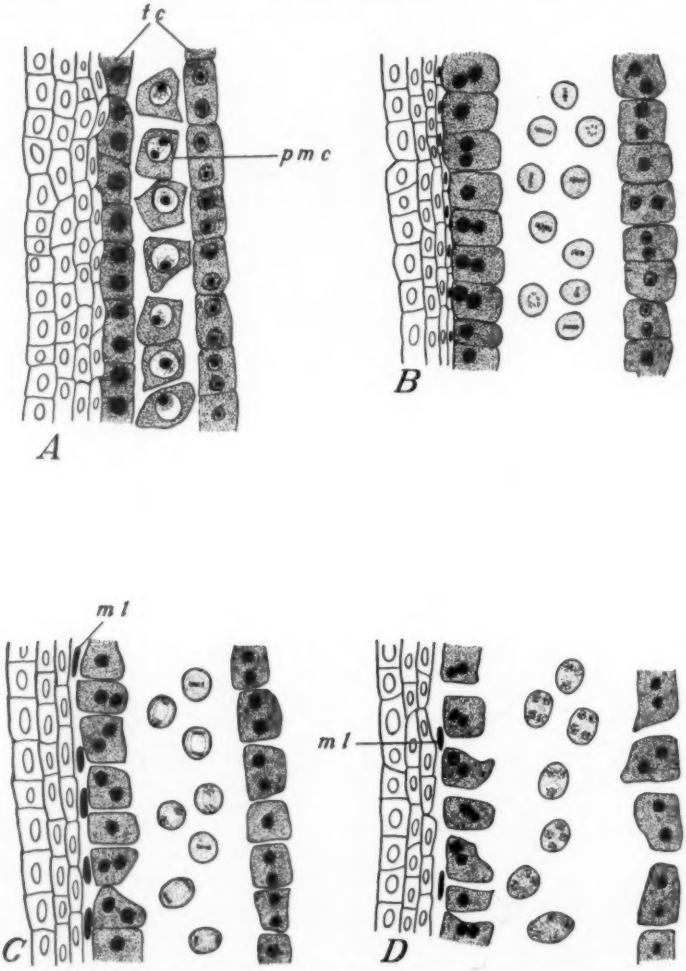
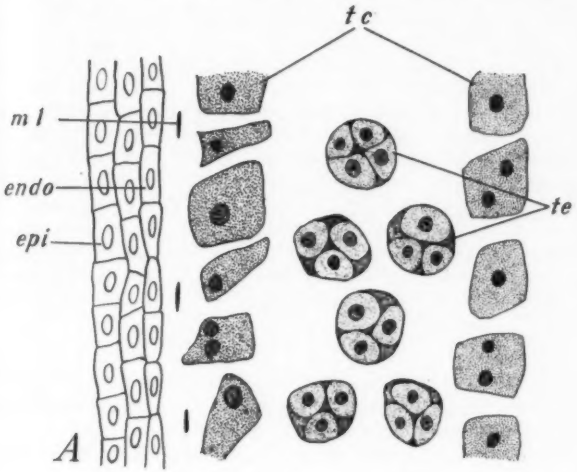



FIGURE 9.—*A*, Pollen mother cells disorganizing. *B*, Metaphase of first meiotic division of pollen mother cells. *C*, Late anaphase of first meiotic division of pollen mother cells; tapetal cells and middle layer degenerating. *D*, Late telophase of second meiotic division of daughter cells. *t c*, Tapetal cells; *p m c*, pollen mother cells; *m l*, middle layer. All × 950.

tained under each of these temperatures. The results of these studies, which have been published elsewhere (*9*), show that anthesis occurred sooner at the higher temperatures to which the plants were exposed. At 50° to 60° the time that elapsed between seeding and anthesis

was 135 days, whereas at 90° to 100° it was only 55 days. Anthesis resulted in 84 days at 60° to 70° and in 73 days at 70° to 80°. Similar



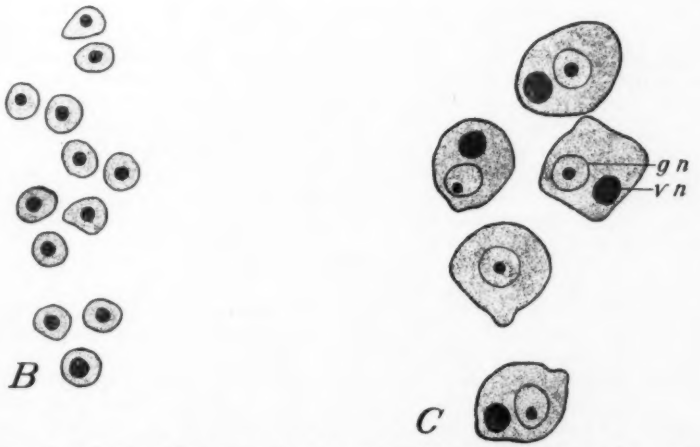




FIGURE 10.—*A*, Tetrads enclosed within the walls of the pollen mother cell. × 950. *B*, Young pollen grains just after being freed from tetrad encasement. × 640. *C*, Mature pollen grains showing one generative and one vegetative nucleus. × 950. *m l*, Middle layer; *endo*, endothecium; *epi*, epidermis; *tc*, tapetal cells; *te*, tetrad; *g n*, generative nucleus; *v n*, vegetative nucleus.

results with tomato have been reported by Smith (*22*). Anthesis occurred 10 days earlier under a 10-hour day than under a 14-hour

day. Pepper is therefore a "short-day" type of plant, as the term is used for plants that produce their flower primordia in response to short-day conditions.

Erwin (*14*) made an interesting and thorough study to determine at what time during the day anthesis occurs in the pepper, and he concluded that the major portion of the blossoms open within 3 hours after sunrise. Similar results have been obtained by the writer and by Deshpande (*12*). The period of anthesis in the pepper is comparatively short. Dehiscence normally follows anthesis very closely, and in some cases is simultaneous with it. Under ordinary growing conditions, the petals begin to wither sometime during the second day and usually drop within 2 or 3 days thereafter. Temperatures lower than 75° F., however, materially slow-up the whole mechanism of anthesis and dehiscence. These findings are substantiated by Shaw and Khan (*20*), who further observed that the mechanism in pepper is delayed on cloudy as well as on cold days.

## POLLINATION

The flowers are usually self-pollinated, although some cross-pollination may occur. In fact, since Martin et al. (*18*) have found that *Capsicum* blossoms secrete nectar, which attracts various insects, one is led to believe that cross-pollination takes place more frequently than has generally been supposed. Results of experiments conducted by Erwin (*14*) at Ames and Muscatine, Iowa, show that either self- or cross-pollination may occur. Similar observations have been made in years past at the Georgia Experiment Station.

After the pollen is deposited on the stigma it remains inactive for a short time under all environmental conditions. However, the most rapid and the highest percentage of pollen germination takes place at temperatures ranging from 70° to 85° F. accompanied by a rather high relative humidity. These results are well in accord with those reported by Smith and Cochran (*24*) for the tomato.

Blossoms produced under excessively high temperatures (90° to 100° F.) and low humidity practically always have elongated styles. This elongation occurs well in advance of anther dehiscence, which, in this case, makes self-pollination unlikely. Observations made by Burk (*5*) on the tomato show that length of photoperiod also affects style length, the style being longer under long, than under short-day conditions.

## FERTILIZATION

The time that elapses between pollination and fertilization varies with the temperature to which the plants are subjected. Blossoms that were hand-pollinated in the 70° to 80° F. greenhouse and the plants transferred to the 50° to 60° greenhouse produced practically all parthenocarpic fruits. Examination of slides made of some of these styles show that parthenocarpy was not due to a lack of pollen germination. Because of the lower temperature the pollen tubes failed to reach the embryo sac. No tubes longer than 2 mm were found.

The pollen tubes grow down through the tissue of the style. At some time during the growth of the pollen tubes, the generative nucleus divides, forming two microgametes. The pollen tube ex-

tends through the micropyle, passing between the two synergids and comes to rest near the egg. The actual discharge of the male nuclei was not observed because of the deeply staining contents of the pollen tube. One nucleus fuses with the egg to form the embryo while the other unites with the two polar nuclei to form the primary endosperm nucleus. The embryo sac at the time of fertilization, which at a temperature of 70° to 80° F. was 42 hours after pollination, is shown in figure 8, *A*. At no time was fertilization observed earlier than 42 hours after pollination. The time elapsed between pollination and fertilization is somewhat shorter than that found by Smith (*22*, *23*) for tomato and by East and Park (*13*) for *Nicotiana*. These differences may be due to differences in the length of the style in the three genera. The style of the pepper averages only 4.5 mm in length, that of the tomato 6.75 mm, and that of *Nicotiana* even longer. No doubt, too, the various temperatures under which the respective plants were grown influenced the time element in fertilization.

## DEVELOPMENT OF THE EMBRYO

Apparently Tognini (*27*) made the earliest study of embryo development in the Solanaceae. His study was not complete, including only a few stages of the development of the embryo in *Atropa belladonna*, *Datura stramonium*, *Physalis edulis* and *Solanum tuberosum*.

Souèges (*26*), working with *Atropa belladonna*, *Datura stramonium*, *Hyoscyamus niger*, *Nicotiana acuminata*, *N. sanguinea*, *N. tabacum*, *Solanum dulcamara*, *S. nigrum*, *S. sisymbriifolium*, and *S. villosum*, has reported the most complete study of the embryogeny of the Solanaceae. He found in all of these species that the typical four-celled embryo has its cells arranged in linear order, and these findings are supported by the work of Smith (*23*) with tomato, Bhaduri (*4*) with *Nicotiana plumbaginifolia*, *Petunia nyctaginiflora*, *Physalis minima*, and *Withania somnifera*, and by the present investigation.

After fertilization, the zygote remains in a state of rest for 24 to 36 hours before division starts (fig. 11, *A*). Development of the zygote begins with an enlargement of the embryo sac, especially in length (fig. 11, *B*; fig. 12, *A*). The first division of the young embryo (fig. 12, *B*) is transverse. The two daughter cells then divide transversely, forming a four-celled linear embryo (fig. 12, *C*). In the pepper each cell of the four-celled embryo gives rise to certain definite portions of the mature embryo, but an exception to this has been observed by Bhaduri (*4*) in *Physalis minima*. In the present study, it was found that the cotyledons are derived from the apical cell; the hypocotyl, the initials of the central cylinder, and the cortex of the root tip from the cell just below it; the root-cap primordium and upper part of the suspensor from the next lower cell; and the remaining part of the suspensor from the basal cell. Further development of the embryo is shown in figure 12, *D-J*. As is noted in figure 12, *E* and *F*, the two apical cells *a* and *b* first divide longitudinally, whereas *c* and *d* divide transversely, thus forming an eight-celled embryo, six cells in length. The next division is periclinal, which gives rise to both an outer and an inner group of cells (fig. 12, *G*). The outer cells form the dermatogen while the inner ones divide transversely, separating the initials of the hypocotyl and the radicle. In figure 12,

*J*, the dermatogen, the periblem, the periblem initials, and the plerome have differentiated.

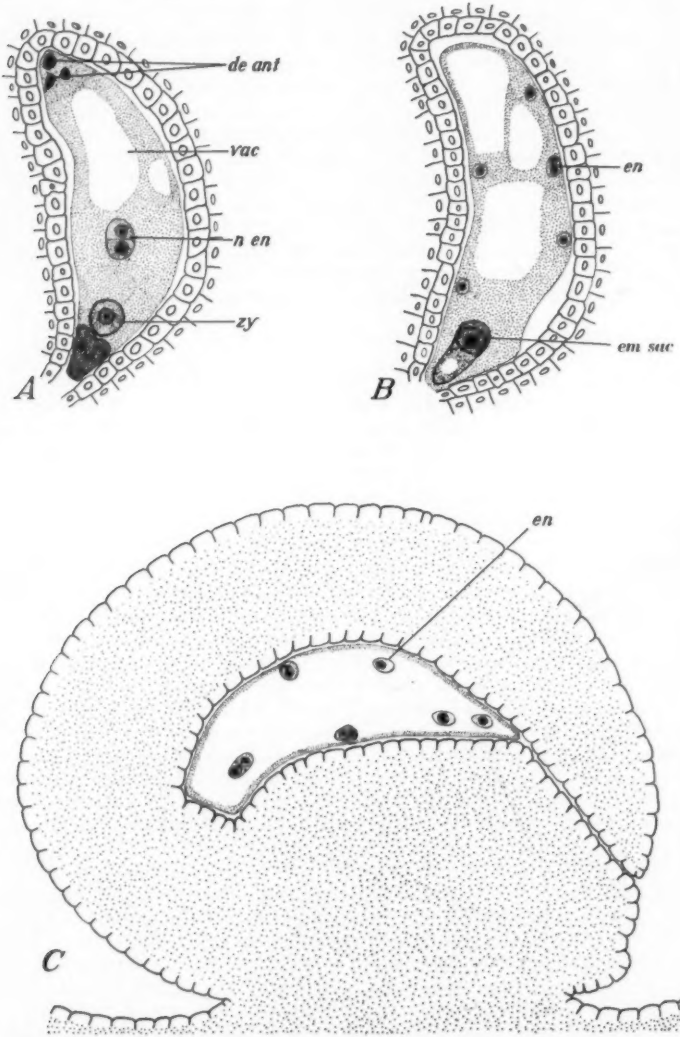



FIGURE 11.—*A*, Fertilized egg in resting stage; endosperm nuclei prior to division; antipodals degenerating. × 950. *B*, Young zygote increasing in size prior to division; endosperm nuclei divided and migrated to periphery of embryo sac. × 950. *C*, Ovule showing endosperm nuclei undergoing division. × 640. *de ant*, Degenerating antipodals; *vac*, vacuole; *n en*, nascent endosperm; *zy*, zygote; *em sac*, embryo sac; *en*, endosperm.

A longitudinal section of the basal tip of the embryo, when the fruit is in the red-ripe stage of maturity shows the root cap, the

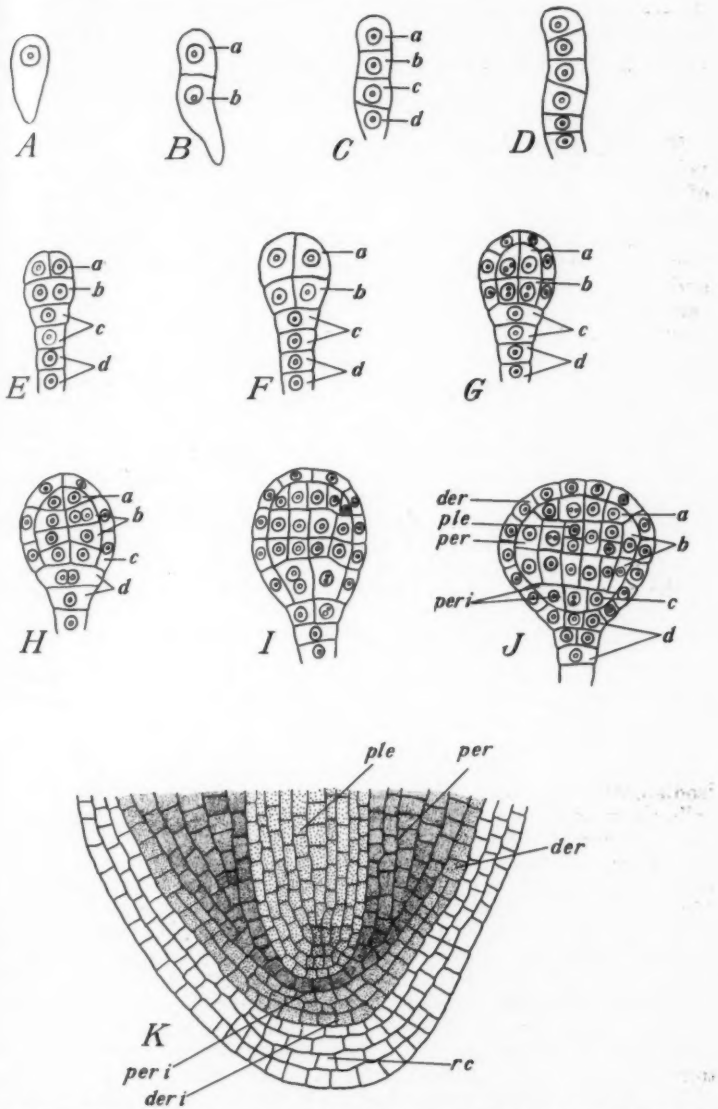



FIGURE 12.—*A*, Young zygote a few hours prior to the first transverse division. × 950. *B–E*, Development of embryo to two, four, six, and eight-nucleate stages respectively. × 950. *F*, Further division of the octant stage. × 950. *G*, Embryo with dermatogen cells cut off in tiers *a* and *b*. × 950. *H*, Embryo showing differentiation of initials of hypocotyl and root tip. × 950. *I*, Further development of embryo as shown in *H*. × 950. *J*, Embryo with dermatogen, periblem, periblem initials, and plerome differentiated. × 950. *K*, Longitudinal section of basal end of a practically mature embryo showing dermatogen, periblem, plerome, periblem initials, dermatogen initials, and root cap. × 440. *der*, Dermatogen; *ple*, plerome; *per*, periblem; *per i*, periblem initials; *der i*, dermatogen initials; *r c*, root cap.

62230—38——2

dermatogen, the periblem, and the plerome (fig. 12, *K*). Further growth of the embryo and the endosperm is shown in figure 13 *A–F*, figure 14, *A–D*, and figure 15, *A–C*.

## DEVELOPMENT OF THE ENDOSPERM

The primary endosperm nucleus, formed by the union of the fused polars with the second male nucleus, begins to divide well in advance of that of the zygote (fig. 11, *B*). The nuclei migrate toward the periphery (fig. 11, *B* and *C*), where they continue to divide very rapidly, soon completely filling the embryo sac. With the rapid growth of the embryo, a portion of the endosperm is gradually digested and apparently absorbed. However, this process is so slow that it cannot be readily detected until approximately 20 to 25 days after pollination. Prior to and including this stage of development, both the endosperm and the embryo cells are well filled with reserve food. Evidently the young seedling is able to use this material until it begins to manufacture its own food. The inner epidermal layer of the integument, which in all probability also aids in nourishing the embryo, is easily recognized and persists until the cotyledons are well-differentiated (fig. 15, *A*, *B*). It is the opinion of Souèges (*25*) that the inner epidermal layer secretes diastase, which causes, the central part of the integument to break down and subsequently disappear. After a lapse of 30 days following pollination, the rate of endosperm absorption increases with the increase in size of the embryo. At maturity of the seed, however, a large portion of the endosperm still remains (fig. 15, *C*).

## DEVELOPMENT OF THE INTEGUMENT

The integument may be detected during the early developmental stages of the young ovule. Usually it makes its first appearance soon after the differentiation of the archesporial cell (fig. 5, *B*, *C*) and portions of it persist throughout seed maturity. Two days after pollination, the outer epidermal cells of the integument are practically isodiametric (fig. 16, *A*). However, as the fruit and seed mature, the cells elongate radially (fig. 16, *B*). Within 25 days after pollination, heavy thickenings are formed on the lateral walls (fig. 16, *C*). These thickenings continue to grow with the development of the seed, finally reaching their maximum size about 30 days after pollination (fig. 16, *D*). The thickenings are characteristically larger at the base of the walls than at any other point and become smaller as they extend toward the outer wall. These findings are confirmed by the earlier work of Hanausek (*16*), Hartwich (*17*), and Souèges (*25*). Unlike the thickenings in tomato (Souèges (*25*), Smith (*23*), those in pepper extend the entire length of the lateral walls, and a smaller proportion of the integument degenerates in the pepper than in the tomato. As a result of this there are small depressions on the surface of the pepper seed, whereas on the tomato seed there are long hairs. In cross section, the thickenings are irregular and wavy in outline (fig. 16, *E*).

## SUMMARY

In the development of the pepper flower, the first primordial whorl to appear is that of the sepals. The remaining three whorls of organs appear in the order of petals, stamens, and carpels.

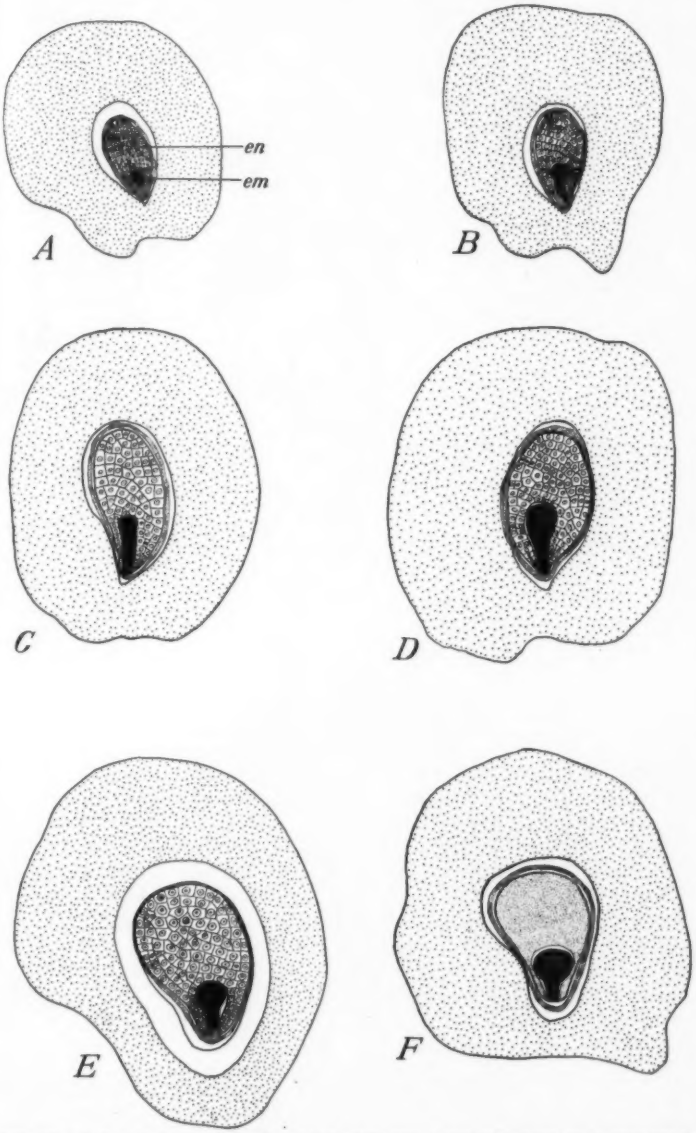



FIGURE 13.—*A–F*, Relative growth of embryo and endosperm; *A*, longitudinal section of young two-celled embryo 72 hours after pollination; *B*, *C*, *D*, *E*, *F*, ovule 5, 7, 9, 11, and 13 days respectively after pollination; *en*, endosperm; *em*, embryo. All × 225.

The young ovule arises from the placental tissue as a small erect protuberance, but subsequently becomes anatropous in form. Early in the development of the ovule, a single hypodermal cell of the

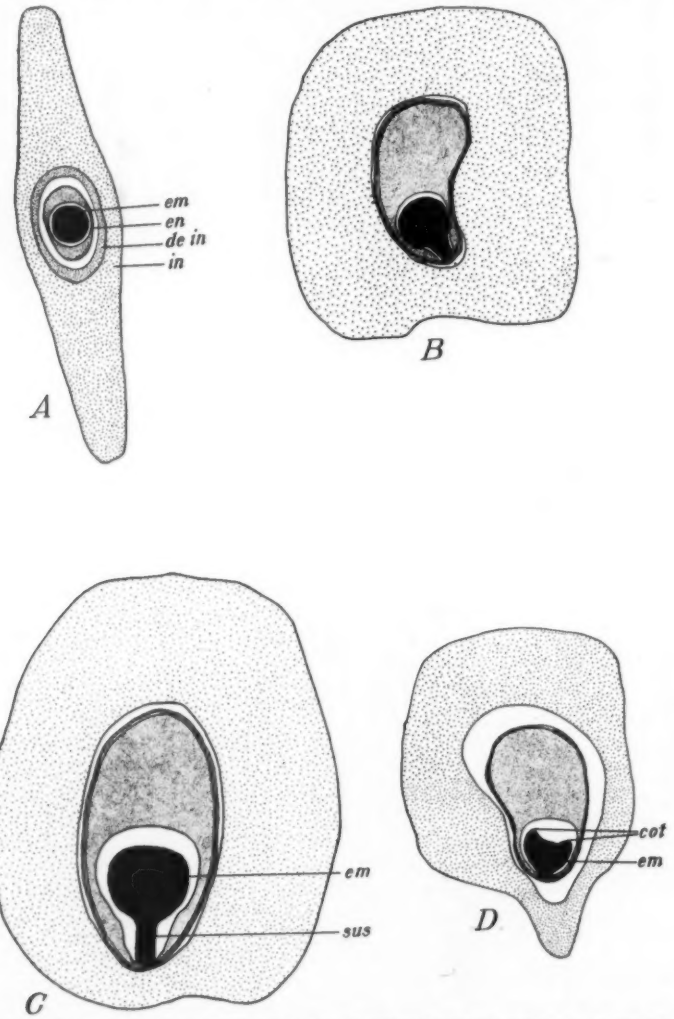



FIGURE 14.—*A*, Transverse section of young ovule showing embryo 13 days after pollination; *B*, longitudinal section of young ovule 15 days after pollination; *C*, ovule 17 days after pollination; *D*, ovule 21 days after pollination, showing initiation of cotyledons; *em*, embryo; *en*, endosperm; *de in*, degenerating portion of integument; *in*, integument; *sus*, suspensor; *cot*, cotyledons. All × 225.

nucellus is differentiated as the archesporial cell, which in this case functions as the macrospore mother cell. By two divisions, the macrospore mother cell forms a linear row of four macrospores of

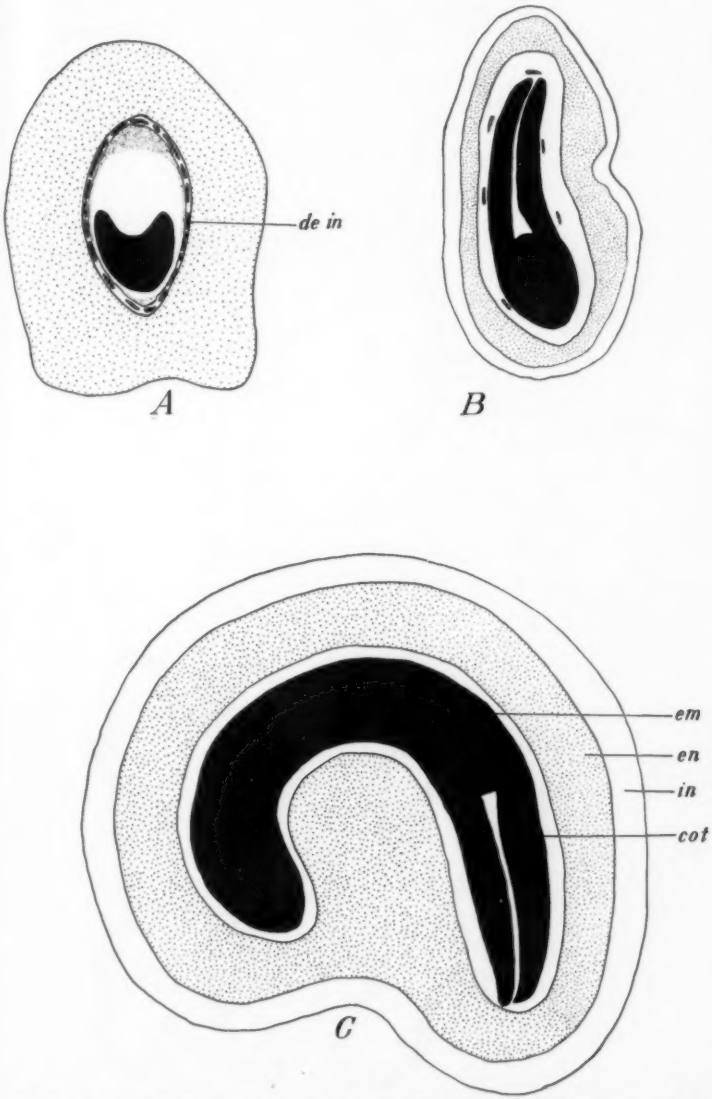



FIGURE 15.—*A*. Longitudinal section of ovule 24 days after pollination, showing development of cotyledons and degeneration portion of integument; *B*, ovule 30 days after pollination, showing further development of cotyledons; inner layer of integument almost completely degenerated; *C*, ovule 40 days after pollination, showing mature embryo; *de in*, degenerating portion of integument; *em*, embryo; *en*, endosperm; *in*, integument; *cot*, cotyledons. All × 225.

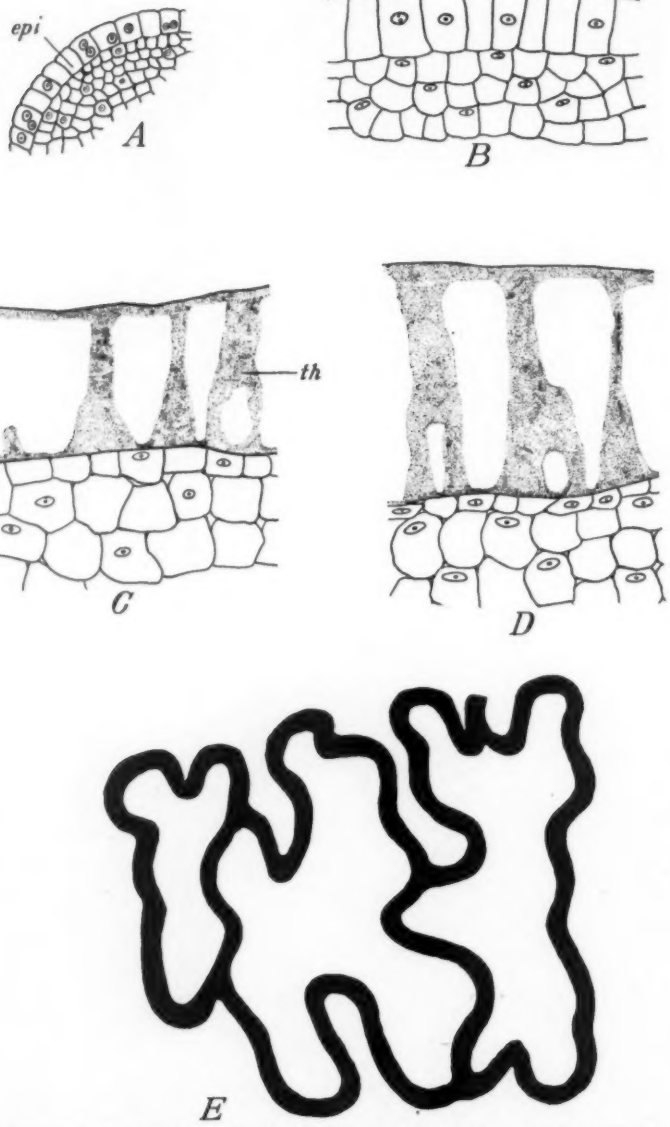



FIGURE 16.—*A*, Outer epidermis and adjacent cells of integument 2 days after pollination, × 750; *B*, outer epidermis of integument showing radial elongation of epidermal cells, × 750; *C*, longitudinal section of epidermis of integument, showing thickenings on lateral walls 25 days after pollination, × 950; *D*, longitudinal section of epidermis of integument, showing thickenings on lateral walls 30 days after pollination, × 950; *E*, transverse section near base of thickenings 36 days after pollination, × 950; *epi*, epidermis; *th*, thickenings.

approximately the same size. The three macropsores nearest the micropyle soon degenerate, leaving the chalazal one which enlarges and becomes functional. By three successive divisions of the functional macrospore, the typical eight-nucleate or mature embryo sac is formed. Two of the nuclei take a position near the center of the sac and become the polars; three migrate to the chalazal end of the sac and become the nuclei of the antipodal cells; the three remaining nuclei take a position near the micropylar end of the sac; the two more pear-shaped ones become the synergids, and the remaining one the egg. The antipodal cells subsequently completely degenerate as do those of the nucellus.

Pollen mother cells arise as a result of periclinal division of the hypodermal archesporial cells that form within the young anther. Each pollen mother cell, by two divisions, forms a tetrad of microspores. The sister cell of the pollen mother cell gives rise to the tapetum, the middle layer, and the endothecium. Mature pollen grains are two-nucleate, containing a spherical generative nucleus and a spherical vegetative nucleus. The generative cell divides to form two male gametes within the growing pollen tube before it reaches the embryo sac. One gamete nucleus unites with the polar nuclei to form the endosperm while the other fuses with the egg to give rise to the embryo.

The higher the temperature to which plants are exposed, up to 90° to 100° F., the more quickly anthesis occurs. Anthesis takes place 10 days earlier under normal-day than under long-day conditions. Dehiscence normally follows anthesis very closely.

The pepper flower is usually self-pollinated.

The time that elapses between pollination and fertilization varies with the temperature to which the blossom is subjected. Fertilization was first observed in the 70° to 80° F. greenhouse 42 hours after pollination.

The zygote does not begin to divide until 24 to 36 hours after fertilization. The first division of the zygote is transverse. The two resulting cells then divide transversely, thus forming a four-celled embryo with its cells arranged in linear order. This arrangement is typical of most members of the Solanaceae. Each cell of the four-celled embryo gives rise to certain definite portions of the mature embryo. The cotyledons are derived from the apical cell; the hypocotyl, the initials of the central cylinder, and the cortex of the root tip from the cell just below it; the root-cap primordium and the upper portion of the suspensor from the next lower cell; and the remaining part of the suspensor from the basal cell.

The endosperm nuclei begin division well in advance of those of the embryo and they soon fill the entire embryo sac. The endosperm is gradually digested and absorbed by the embryo; however, at maturity a large portion of the endosperm still remains.

The outer epidermal cells of the integument are at first isodiametric. As the fruit and seed mature, however, these cells elongate radially as a result of degeneration of tangential walls, and soon thereafter heavy thickenings form at the base of the lateral walls. The thickenings are larger at the base of the walls and become smaller as they extend toward the outer wall.

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# STUDIES ON LONGEVITY AND PRODUCTIVITY IN TRICHOGRAMMA EVANESCENS[1]

By HORACE O. LUND[2]

Formerly *assistant in entomology, Division of Entomology and Economic Zoology, Minnesota Agricultural Experiment Station*

## INTRODUCTION

During recent years entomologists have expended considerable time and ingenuity in an effort to utilize successfully the chalcid egg parasite *Trichogramma* in the biological control of certain insect pests. Since the results of these efforts have not been altogether encouraging, it is hoped that the present study of the influence of certain environmental factors upon the longevity and the productivity of the adult parasites may help to elucidate the problems involved. To date, the only comprehensive work along this line is that published by Schulze (*27*).[3] The results of her work are discussed in connection with the results of the present experiments.

The present paper records the effects of feeding, absence of host eggs, mating, superparasitism, diffused light, temperature, and moisture upon the longevity and productivity of *Trichogramma evanescens* Westwood.

## EXPERIMENTAL PROCEDURE

The Angoumois grain moth, *Sitotroga cerealella* (Oliv.), was chosen as the host in these experiments largely because it is the species most commonly used in mass rearing for pest control. The host insects were reared in shelled corn, and in order to procure the moth eggs for parasitism by *Trichogramma*, several hundred individuals were collected in a quart jar by means of a small suction trap. In this crowded condition, the females readily deposited their eggs, which were easily collected simply by shaking them out through a screen lid (22 meshes to the inch). After the eggs had been cleaned of debris, they were fastened to small bits of paper by means of dilute gum arabic, and each egg paper was labeled with the date, the time, and the number of the vial in which the female parasite being tested was confined. The eggs were then placed in the vial with the parasite for parasitism.

The parasites were reared in small desiccators at 30°, 25°, 20°, 15°, and 10° C. in cabinets regulated by toluene-mercury thermostats, the temperatures of which did not vary significantly more than one-half degree centigrade.

The moisure conditions in the desiccators were controlled by means of ample volumes of sulphuric acid solutions, which were changed frequently and were exposed to the air only as long as was absolutely

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[3] Reference is made by number (italic) to Literature Cited, p. 437.

necessary in making the observations. It is believed that the time required for the atmosphere in the small rearing vials to arrive at an equilibrium with the atmosphere in the desiccators was not significantly long, since the vials were out of the desiccators only a very few minutes either once or twice daily, the desiccators themselves were small, and the tops of the vials were never more than 2½ inches above the surface of the liquid. The desiccators, unless otherwise stated, were covered with a heavy coating of black paint to eliminate any possible effect of light variation.

In testing the effects of temperature, an attempt was made to eliminate moisture as a variable factor, i. e., to maintain moisture conditions such that the total evaporation during the period of exposure would be about the same at each temperature. Mellanby (*18*) points out that this state of affairs is realized only when the products of the exposure times and the saturation deficiencies (expressed in millimeters of mercury) are constant. Such constant products were attained very well at the three higher temperatures used (30°, 25°, and 20° C., where the products were 52.5, 50.0, and 50.0, respectively, for development, and 30.0, 30.0, and 26.2, respectively, for adult longevity), but at 15° and 10°, the use of a sufficiently low saturation deficiency to produce a constant product was deliberately avoided for fear of the development of mold, and, as a consequence, the total evaporation was somewhat greater at the two lower temperatures than at the other temperatures.

The experimental procedure was so planned and controlled that the following facts could be recorded: The conditions under which each immature and adult parasite was reared; the time of emergence of the parent parasites from the host eggs; the time that these recently emerged males and females were placed together; the time during which each batch of fresh host eggs was parasitized; the number of host eggs parasitized in each batch; the sex ratio of the emerged progeny; and the time of death of each parent parasite. (The parasites were considered to be dead when they were no longer able to walk.)

The actual procedure in setting up an experiment was as follows: Fresh host eggs were carefully selected under a binocular dissecting microscope (30×) and transferred individually onto graph paper (lined to one-tenth of an inch), to which they were fastened with dilute gum arabic, according to the method of Salt (*23*). Batches of 100 eggs so arranged were then placed for parasitism in 3- or 4-dram vials stoppered with corks containing ¼-inch perforations covered with silk bolting cloth. These vials were maintained under controlled conditions until the progeny began to emerge. Within 12 hours (24 hours when reared at 20° C. or lower) after the first emerging progeny appeared, the egg papers were removed and each individual parasitized host egg was cut away from the others and dropped into a separate ½-dram vial stoppered with a cork containing a ⅛-inch perforation covered with silk bolting cloth. These vials were then replaced immediately in the original condition, where the parasites completed their development, each vial being checked at intervals of 12 or 24 hours for the emerged parasite. On emergence of the parasite, the vial was emptied of its host-egg paper and numbered. The parasites were then fed, paired, given host eggs, etc., as desired and placed under the environmental conditions in which it was intended that the adults should live and die.

Each 12 or 24 hours until death, fresh moth eggs were presented to each female for parasitism. At the same time, the previous paper of eggs was removed and placed at a uniformly favorable condition of 25° C. and 5-mm saturating deficiency (hereafter referred to as the "standard condition") for the incubation of the contained parasites. In order to make sure that the maximum capabilities of the females under the particular conditions were being expressed, many more host eggs were presented in each case than could possibly be parasitized.

After about 2 weeks (ample time for the parasite progeny to emerge and die) the egg papers were removed from the incubation vials and the parasitized host eggs on each paper counted. This was accomplished readily because of the fact that parasitized *Sitotroga* eggs invariably turn black. The number of blackened host eggs was taken to represent the productivity of the female parasites. This being the case, it should be mentioned that in the writer's experience, *Sitotroga* eggs turn black only when parasitized. In several thousand black host eggs dissected, all contained parasites. Furthermore, it is fairly safe to assume that each blackened host egg contained only 1 parasite, since only 5 of 520 (0.96%) parasitized *Sitotroga* eggs cleared in lactophenol solution contained two developing parasites, and Salt (*24*) has shown that *T. evanescens* definitely avoids superparasitism—especially when an abundance of host material is present. It is true, however, that some of the parasite progeny deposited in host eggs may have died, for some reason or other, before they reached the late larval or early pupal stage (at which time, apparently, they cause the coloring of the host egg) and therefore failed to leave visible evidence of their having been produced. The female parasites received credit in these experiments, therefore, for only the number of their progeny that completed 2 or 3 days of development under the standard condition.

At the same time that the parasitized host eggs were counted, the emerged parasite progeny were removed to a drop of clear mineral oil, where they could be manipulated conveniently under a microscope and the sex determined. The sex ratio in *Trichogramma* is a convenient indicator of whether or not a particular female has been impregnated, since virgin females produce only male offspring. Thus the partical or complete impotence of the male is reflected in an abnormally low sex ratio.

## LONGEVITY AND PRODUCTIVITY AT THE STANDARD CONDITION (25° C. AND 5-MM SATURATION DEFICIENCY)

The insects considered in this section were kept at the standard condition throughout both their developmental and adult periods. The data on the average longevity of isolated pairs of honey-fed males and females and the number of progeny produced by them when they were given fresh host eggs in which to oviposit immediately after pairing and at regular half-day intervals thereafter until death, are summarized in table 1.

The figure $66.1 \pm 2.5$ for the number of progeny per female is considerably larger than that given by Schulze (*27*), who found a mean of 43.2 parasitized *Ephestia* eggs per female. This discrepancy in results may be due to a difference in method, host, or strain of parasites.

TABLE 1.—*Productivity (host eggs turning black) and longevity of fed pairs at 25° C. and 5-mm saturation deficiency*

| Item | $N$ [1] | Range | Mean ± S. E. | C. V. |
|---|---|---|---|---|
| Progeny.....number.. | 70 | 15–114 | 66. 1±2. 5 | 31. 8 |
| ♀ longevity.....days.. | 71 | 1–13 | 6. 3± . 3 | 46. 6 |
| ♂ longevity.....do.... | 63 | 1–9. 5 | 5. 7± . 2 | 30. 3 |

[1] Number of parasites tested.

Bowen (*6*) reared what is probably *Trichogramma evanescens* (see Flanders (*11*)), at room temperature (75°–80° F.) in bagworm eggs (*Thyridopteryx ephemeraeformis* (Haw.)) and found that 42 females averaged 37.0±2.1 progeny, a figure that approximates that given by Schulze. The difference between this figure and that given in table 1 is very probably due also to the differences in host and method.

The distribution of the egg laying through the life of the female is indicated in figure 1.

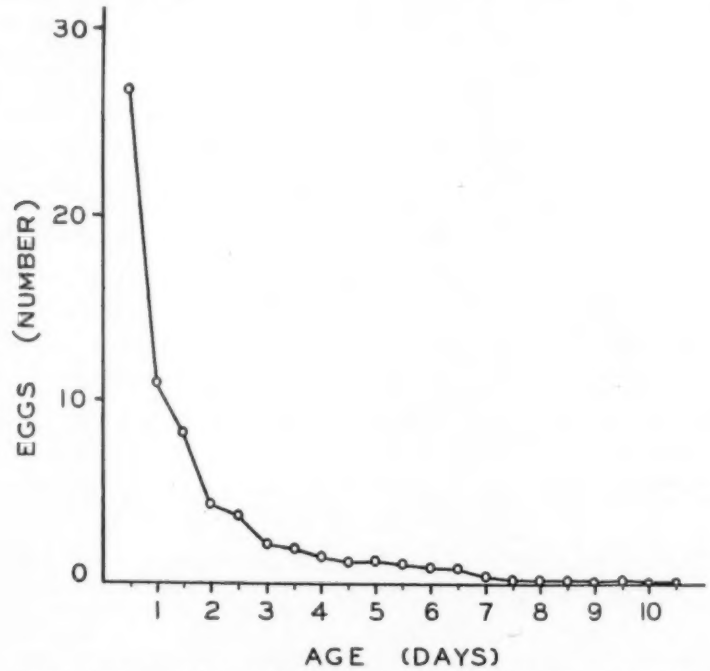


FIGURE 1.—Eggs laid as related to age of adult when kept at 25° C. and 5-mm saturation deficiency.

It will be noticed that almost half (26.75 eggs or 40.5 percent) of the total number of eggs is produced during the first 12 hours of the female's life. This curve differs from the one given by Schulze in that it indicates no rise in the number of progeny produced after the fifth day.

The longevity of mated and fed females reared in *Sitotroga* eggs at 25° C. is 6.3±0.3, with a range of 1 to 13 days. Schulze gives the figure as 13 days, but presents none of the data used in arriving at that figure. Bowen gives the figure as 5.17±0.29 days based upon 42 females reared in *Ephestia* eggs. The writer found that the longevity of paired, fed males is 5.7±0.2 days, not significantly different from the figure for the females. Most of the males die between the fifth and seventh days after emergence however, whereas death of the females is more evenly distributed between the extremes of the life span. This greater spread in length of life of the females is also shown by their coefficient of variation (table 1).

The sex ratio of 1,788 progeny from females paired with males is 0.66 female, the ratio remaining about constant throughout the period of production.

When the longevity of the mated females is correlated with their egg production, a significantly high correlation coefficient of +0.639± 0.071 is obtained. This is explained best by assuming that the longer lived females are fundamentally capable of greater egg production, and not merely that they have more time in which to lay eggs. This must be true since during the first 2 days 76.0 percent of the eggs are produced, at the end of which time 92.9 percent of all the females are still living. In other words, high total egg production is correlated with high production in the initial period of egg laying. Thus the 36 highest producers (averaging 82.2 total progeny per female) produced 57.9 progeny the first 2 days of production; while the lowest 34 producers (averaging 49.1 total progeny per female) produced only 40.8 progeny during the first 2 days.

## INFLUENCE OF DIFFERENT FACTORS ON LONGEVITY AND PRODUCTIVITY

### EFFECTS OF FEEDING

At the standard condition, those adult parasites that were fed on dilute honey placed in a thin streak on the inside of each vial, lived significantly longer than starved parasites. This was true of isolated females, isolated males, male-female pairs, and female-female pairs—whether host eggs were available or not. In all cases, moreover, fed females produced significantly more progeny than starved females. The data for virgin females in table 2 are representative of the results obtained in all the combinations tried.

TABLE 2.—*Productivity (black host eggs) and longevity of fed and unfed virgin females*

| Item | Fed virgins | | Unfed virgins | | Fed virgins minus unfed virgins | |
|---|---|---|---|---|---|---|
| | *N* | Mean± S. E. | *N* | Mean± S. E. | Difference± S. E. | Difference / S. E. difference |
| Progeny, number | 95 | 81.5±2.2 | 79 | 60.8±1.7 | 20.7±2.8 | 7.4 |
| Longevity, days | 93 | 6.4±.3 | 79 | 3.3±.1 | 3.1±.3 | 10.3 |

These data confirm, in general, the findings of Schulze (*27*), Peterson (*21*), and List and Davis (*15*) and indicate that feeding the parasites before liberation in the field will heighten their effectiveness by increasing both their longevity and their productivity.

### EFFECTS OF WITHHOLDING HOST EGGS

In these experiments, conducted at the standard condition, host eggs were withheld from fed virgin females for 48 hours, for 72 hours, and for the entire duration of the life of the female. In table 3 longevity and productivity of the females under each of these conditions are compared with those of females that were kept in the presence of fresh host eggs throughout their lives.

It is evident that virgin females live longer in the presence of host eggs than in their complete absence. This is in accordance with the findings of Hase (*13*), who suggests that the longer life in the presence of host eggs may be due to the habit of the female of feeding on the minute droplet of liquid exuding from the puncture in the chorion of the host egg from which she has just withdrawn her ovipositor, and may explain in part the pronounced effectiveness of the parasites in the field in times of host abundance and their utter ineffectiveness in times of moderate or meager host abundance, since the finding of a readily available host egg by the female parasite in itself increases her effectiveness by lengthening her life.

On the other hand, if the host eggs are withheld from virgin females for 48 or for 72 hours, longevity is unaffected, but productivity is significantly reduced. Thus the egg-laying ability of females that are prevented from ovipositing diminishes with increasing age, even though half or two-thirds of their life span remains after the host eggs are given them. Schulze (*27*) found that if females were deprived of host eggs for as long as 5 days, their longevity was not reduced. Since, however, the productivity of females diminishes rapidly after emergence, the advantage of liberating young parasites in field control measures is apparent.

TABLE 3.—*Productivity (black host eggs) and longevity of virgin females given host eggs at once compared with those of females from which host eggs were withheld for various lengths of time*

| Treatment and factors observed | | *N* | Mean± S. E. | Difference± S. E. | Difference / S. E. difference |
|---|---|---|---|---|---|
| Host eggs given at once: | | | | | |
| Progeny | number | 95 | 81. 5±2. 2 (1) | | |
| Longevity | days | 93 | 6. 4±. 3 (1) | | |
| Host eggs withheld 48 hours: | | | | | |
| Progeny | number | 30 | 54. 7±4. 1 (2) | [1] 26. 8±4. 7 | 5. 7 |
| Longevity | days | 30 | 6. 3±. 6 (2) | [1] . 1±. 7 | . 1 |
| Host eggs withheld 72 hours: | | | | | |
| Progeny | number | 23 | 44. 7±4. 2 (3) | [2] 36. 8±4. 8 | 7. 7 |
| Longevity | days | 23 | 7. 3±. 5 (3) | [2] −. 9±. 6 | 1. 5 |
| Host eggs withheld entirely: | | | | | |
| No progeny | | | | | |
| Longevity | days | 31 | 4. 3±. 3 (4) | [3] 2. 1±. 4 | 5. 2 |

[1] (1 minus 2). [2] (1 minus 3). [3] (1 minus 4).

### EFFECTS OF PAIRING

In these experiments the fed females were given host eggs immediately upon emergence but were individually isolated for 24 hours or

for their entire lives at the standard condition. In table 4 the longevity and productivity of these females are compared with those of females kept in the presence of males from the time of emergence until death.

TABLE 4.—*Productivity (black host eggs) and longevity of females paired with males immediately compared with those of females whose pairing was delayed*

| Treatment and factors observed | *N* | Mean±S. E. | Difference± S. E. | Difference / S. E. difference |
|---|---|---|---|---|
| Pairing immediate: | | | | |
| Progeny.....number.. | 70 | 66.1±2.5 (1) | ..... | ..... |
| Longevity.....days.. | 71 | 6.3± .3 (1) | ..... | ..... |
| Pairing delayed 24 hours: | | | | |
| Progeny.....number.. | 25 | 66.8±4.2 (2) | [1] 0.7±4.9 | 0.1 |
| Longevity.....days.. | 25 | 7.0± .6 (2) | [1] .7±.7 | 1.0 |
| Pairing entirely prevented: | | | | |
| Progeny.....number.. | 95 | 81.5±2.2 (3) | [2] 15.4±3.3 | 4.7 |
| Longevity.....days.. | 93 | 6.4±.3 (3) | [2] .1±.4 | .2 |

[1] 2 minus 1. [2] 3 minus 1.

The data in table 4 indicate that, although the longevity of the females is unaffected by pairing, there is a definite increase in the number of progeny when the females remain virgin throughout their lives. Evidently the presence of the male in some way inhibits oviposition. That the mere presence of another insect, rather than the disturbance caused by the act of copulation itself, is responsible for the lower productivity of paired females is suggested by the fact that the presence of a second female has the same effect as the presence of a male ($N=30$; average productivity in female-female pairs= $67.1\pm2.5$).

Schulze (*27*) also found that unimpregnated females produced more progeny than impregnated females (48.4:43.2), and Peterson (*21*) states that unfertilized females produced "as numerous" progeny as did the fertilized. On the other hand, Hanson and Ferris (*12*) found that mated females of *Drosophila melanogaster* Meig., a species that does not reproduce parthenogenetically, lay from 1.6 to 2.0 times more eggs than do virgins, the presence of the male stimulating, rather than inhibiting, oviposition.

Females given host eggs immediately upon emergence but denied the opportunity to mate until they are 24 hours old, do not differ either in longevity or productivity from females mated immediately upon emergence. Males, however, that are denied the opportunity to mate until they are 48 hours old live significantly longer than males paired immediately upon emergence (mean=6.6 days as against 5.9 days; difference S. E. difference=2.9). That male potency is unaffected by this delay in mating is indicated by the fact that a normal proportion of the progeny produced immediately after pairing is made up of females (0.68 female in 1,112 progeny).

### EFFECTS OF SUPERPARASITISM

The data discussed in this section refer to fed pairs, each consisting of a male and a female parasite reared in the same *Sitotroga* egg under the standard condition. The data were assembled from records taken on scattered cases of superparasitism encountered in the course of several experiments, and are presented in table 5.

TABLE 5.—*Productivity (black host eggs) and longevity of pairs reared to maturity in separate host eggs compared with those of pairs reared in the same host egg*

| Item | Pairs from separate host eggs | | Pairs from the same host egg | | Pairs from separate host eggs minus pairs from the same host egg | |
|---|---|---|---|---|---|---|
| | *N* | Mean±S. E. | *N* | Mean±S. E. | Difference± S. E. | Difference / S. E. difference |
| Progeny.....number.. | 70 | 66. 1±2. 5 | 19 | 51. 9±3. 2 | 14. 2±4. 1 | 3. 5 |
| ♀longevity.....days.. | 71 | 6. 3± . 3 | 20 | 6. 6± . 5 | −. 3± . 6 | .5 |
| ♂longevity.....do.... | 63 | 5. 7± . 2 | 17 | 3. 4± . 4 | 2. 3± . 4 | 5. 7 |

While the number of cases is small, it is evident from table 5 that crowding of the immature stages of both male and female into the same host egg significantly reduces the number of progeny. The longevity of the male is reduced while that of the female is unaffected. In all except two of these cases of superparasitism, the male was very small and wingless, while the female, although definitely smaller than her normal sisters, was fully winged and considerably larger than the male. In superparasitized *Sitotroga* eggs the female is apparently able to thrive at the expense of the male. The dwarf males, however, are sexually potent, as is indicated by a very high proportion of female progeny produced by these pairs (sex ratio is 0.82 female in 495 progeny examined).

Paralleling these findings on *T. evanescens* are the data of Alpatov (*1*), who found that undersized females of *Drosophila melanogaster* (larvae taken from their food prematurely) lived just as long as normal females and (*2*) that underfeeding reduced productivity. Norris (*20*) found also that the number of eggs produced by *Ephestia kuehniella* Zell. was reduced by rearing on an abnormally small quantity of food.

### EFFECTS OF DIFFUSED LIGHT

In these experiments, fed virgin females were exposed to a constant diffused light throughout their adult lives at the standard condition. The source of the light was an ordinary Mazda bulb suspended 9 inches above the double-glass top of the temperature cabinet, and the intensity, as measured on a Western Electric photometer, was about 75 foot-candles.

TABLE 6.—*Effect of diffused light upon the productivity (black host eggs) and longevity of isolated virgin females*

| Item | Virgins kept in darkness | | Virgins kept in light | | Virgins in darkness minus virgins in light | |
|---|---|---|---|---|---|---|
| | *N* | Mean±S. E. | *N* | Mean±S. E. | Difference± S. E. | Difference / S. E. difference |
| Progeny.....number.. | 95 | 81. 5±2. 2 | 64 | 76. 8±2. 9 | 4. 7±3. 6 | 1. 3 |
| Longevity.....days.. | 93 | 6. 4± . 3 | 66 | 7. 2± . 3 | −. 8± . 4 | 2. 0 |

It will be seen from table 6 that there is no significant difference between the number of progeny produced by virgins kept in the light

and those kept in the dark, but the longevity of females in the lighted desiccators is slightly greater than that of females kept in the dark. This is contrary to what other workers have found. Thus, Peterson (*21, p. 8*) states: "There is strong evidence in the writer's investigations to show that more eggs are parasitized on bright days than on dull cloudy ones. In artificial production, the correct intensity of light is important." And Flanders (*9*) writes: "Light intensity appears to be the dominating influence in the activity of *Trichogramma*." It may well be that the effects of light and temperature were not differentiated by these observers, but it is also possible that differences in the intensity of the light and its spectral composition may account for the discrepancies between the observations of Peterson and Flanders and those indicated in table 6. The present limited observations, however, suggest that light may be of less importance in artificial rearing than has been supposed.

## EFFECTS OF TEMPERATURE

### Effects of Temperature Acting Upon the Adults

In these experiments, the parasites were all reared from egg to maturity at the standard condition of 25° C. and 5-mm saturation deficiency. Immediately after emergence the adults were fed, paired, and placed at the temperatures indicated in table 7, where they remained for the duration of their lives.

In making the daily observations on the parasites kept at 20°, 15°, and 10° C., the exposure to room temperature averaged somewhat less than 2½ minutes each day, whereas in the experiments run at 25° and 30°, the morning and evening exposure to room temperature totaled less than 10 minutes daily.

Table 7.—*Productivity (black host eggs) and longevity of pairs at successive 5° temperature intervals*

| Treatment and factors observed [1] | *N* | Mean±S. E. | Difference± S. E. | Difference / S. E. difference |
|---|---|---|---|---|
| 30° (7.5 mm): | | | | |
| Progeny.....number | 90 | 63. 2±1. 6 | | |
| ♀ longevity.....days | 90 | 4. 1± .1 | | |
| ♂ longevity.....do | 87 | 3. 6± .1 | | |
| 25° (5.0 mm): | | | | |
| Progeny.....number | 70 | 61. 1±2. 5 | [2] 2. 9±3. 0 | 1.0 |
| ♀ longevity.....days | 71 | 6. 3± .3 | [2] 2. 2± .3 | 7.3 |
| ♂ longevity.....do | 63 | 5. 7± .2 | [2] 2. 1± .2 | 10.5 |
| 19° (2.5 mm): | | | | |
| Progeny.....number | 120 | 61. 9±1. 4 | [3]−4. 2±2. 9 | 1.4 |
| ♀ longevity.....days | 119 | 11. 2± .3 | [3] 4. 9± .4 | 12.2 |
| ♂ longevity.....do | 119 | 10. 1± .2 | [3] 4. 4± .3 | 14.7 |
| 15° (2.5 mm): | | | | |
| Progeny.....number | 68 | 46. 3±2. 4 | [4]−15. 6±2. 8 | 5.6 |
| ♀ longevity.....days | 68 | 15. 2± .6 | [4] 4. 0± .7 | 5.7 |
| ♂ longevity.....do | 68 | 15. 1± .7 | [4] 5. 0± .7 | 7.1 |
| 10° (2.5 mm): | | | | |
| Progeny.....number | 60 | 1. 2− | | |
| ♀ longevity.....days | 60 | 17. 5± .7 | [5] 2. 3± .9 | 2.5 |
| ♂ longevity.....do | 59 | 14. 7± .6 | [5]−. 4± .9 | .4 |

[1] Temperature in degrees centigrade. Saturation deficiencies in millimeters of mercury.
[2] 25° minus 30°.
[3] 20° minus 25°.
[4] 15° minus 20°.
[5] 10° minus 15°.

It will be noticed from table 7 that the longevity of the adults is inversely related to the temperature down to 15° C., below which life is scarcely, if at all, prolonged. The number of progeny produced holds a fairly constant level from 30° down to 20°, but drops off sharply below this. From general work on temperature optima, however, it seems likely that a more or less definite optimum point for egg production in *Trichogramma* lies somewhere between 30° and 25°. It would appear that 10° is about the lowest temperature at which the mechanism of oviposition in *T. evanescens* can function.

Although Schulze (*27*) does not state the number of cases upon which her data are based nor the humidity conditions to which the parasites were exposed, she gives the average longevity of *Trichogramma* at 25° C. as 13 days, and at 29.5° as 5 days. Both of these figures are considerably larger than the corresponding figures in table 7.

Schulze's figures for productivity at different temperatures (10.0 at 15° C. and 34.0 at 29.7°) are much lower than those in table 7. This is probably due to the fact that she incubated the parasitized host eggs at the temperature at which parasitism took place. Thus she measured the effects of adverse temperatures upon both egg production and egg development rather than upon egg production alone. She used *Ephestia* eggs rather than *Sitotroga* eggs as host material.

Data are given by van Steenburgh (*28*) for 12 isolated females of a "gray strain" (probably *T. evanescens*) kept at each of four temperatures roughly comparable to those given in table 7. The wide discrepancies in results would certainly seem to indicate that some gross difference in species or method must exist.

The general fact illustrated here of the increase in adult longevity in insects with a decrease in the temperature to which the adults are exposed was pointed out by Pictet as early as 1913 (cited by Uvarov (*30*) and by Baumberger (*4*) in 1914. This same relationship was found to be true for *Drosophila* by Loeb and Northrop (*16*, *17*) and Alpatov and Pearl (*3*), and for several species of insects by Janisch (*14*).

From table 7 it will be noticed that at all temperatures the females live longer than the males (ratios of mean differences to the standard errors of the differences at 30° and 20° C. are 3.3 and 3.0, respectively); but at 25° and 15° the differences are statistically insignificant. It seems likely that the general rule is a greater longevity in the females than in the males, even though the data at 25° and 15° are not convincing on this point.

The existence of an optimum temperature for egg production in insects has been recognized for some time. This is indicated, for example, in the work of Ewing (*8*) on *Aphis avenae* Fab.; Titschak (*29*) on *Tineola biselliella* (Hum.); Schubert (*26*) on *Piesma quadrata* Fieb.; and Menusan (*19*) on *Acanthocelides obtectus* (Say).

As for the distribution of the egg laying throughout the lives of the females included in the present study, it may be said that the number of progeny produced on the first day varies directly with the temperature, the oviposition tending to stretch out over a longer period at the lower temperatures.

Table 8 indicates the relative numbers of females produced by parasites kept at the different temperatures. It would appear that any variation from 25° C. lowers the relative number of females. The explanation probably lines in a differential stimulation or inhibition of copulation or oviposition rate.

TABLE 8.—*Sex ratios of the progeny of pairs placed at different temperatures immediately after emergence*

| Temperature (° C.) | ♀/total | Total counted |
|---|---|---|
| 30 | 0.43 | 4,232 |
| 25 | .66 | 1,788 |
| 20 | .52 | 5,520 |
| 15 | .37 | 2,603 |
| 10 | .28 | 57 |

Since the insects live much longer at 20° than at 30° C. (and length of life is certainly a variable upon which the ability of the parasite to find its hosts is at least partially dependent) and since the difference in productivity at the two temperatures is relatively small, there would seem to be some advantage in liberating the parasites for inundative field control (Flanders (*10*)) when the temperature is between 20° and 25° rather than 25° to 30° or higher.

### EFFECTS OF TEMPERATURE ACTING UPON THE IMMATURE STAGES IN THE HOST EGGS

In the experiments treated in this section, the *Trichogramma* were reared to maturity at 30°, 25°, 20°, or 15° C. but were allowed to spend their adult lives at the standard condition of 25° and 5-mm saturation deficiency. Thus the influence of these several temperatures upon the development of the sexual functions and products was tested at a single temperature. The effects of a temperature of 10° acting upon the immature forms could not be determined, since about 900 parasitized host eggs failed to produce a single adult at this temperature.

It will be noticed in table 9 that the longevity of both males and females at the standard condition is reduced as the temperature at which the immature stages are kept is lowered. On the other hand, rearing at either higher or lower temperatures than 25° C. reduces the subsequent productivity at the standard condition.

TABLE 9.—*Productivity (black host eggs) and longevity at 25° C. of pairs reared to maturity at different temperatures*

| Treatment and factors observed [1] | *N* | Mean±S. E. | Difference±S. E. | Difference / S. E. difference |
|---|---|---|---|---|
| 30° (7.5 mm): | | | | |
| Progeny ..... number | 39 | 53.5±4.3 | ..... | ..... |
| ♀ longevity ..... days | 38 | 7.9±.3 | ..... | ..... |
| ♂ longevity ..... do | 37 | 6.8±.3 | ..... | ..... |
| 25° (5.0 mm): | | | | |
| Progeny ..... number | 70 | 66.1±2.5 | [2] −12.6±4.9 | 2.6 |
| ♀ longevity ..... days | 71 | 6.3±.3 | [2] 1.6±.4 | 4.0 |
| ♂ longevity ..... do | 63 | 5.7±.2 | [2] 1.1±.4 | 2.7 |
| 20° (2.5 mm): | | | | |
| Progeny ..... number | 65 | 57.9±1.8 | [3] 8.2±3.1 | 2.6 |
| ♀ longevity ..... days | 65 | 6.2±.3 | [3] 0.1±.4 | .2 |
| ♂ longevity ..... do | 67 | 5.6±.2 | [3] 0.1±.3 | .3 |
| 15° (2.5 mm): | | | | |
| Progeny ..... number | 113 | 28.3±1.1 | [4] 19.6±2.1 | 9.3 |
| ♀ longevity ..... days | 113 | 4.7±.2 | [4] 1.5±.4 | 3.7 |
| ♂ longevity ..... do | 110 | 4.5±.1 | [4] 1.1±.2 | 5.5 |

[1] Temperature in degrees centigrade. Saturation deficiencies in millimeters of mercury.
[2] 30° minus 25°.
[3] 25° minus 20°.
[4] 20° minus 15°.

*Trichogramma* adults are extremely active at 25° C. after they have been reared to maturity at 15°. The physiological explanation of this excessive activity is not apparent, but it may partly account for the short lives of the adults.

Apparently very few attempts have been made to distinguish between the effects of temperature upon the development of the sexual functions or products and upon the immediate expression of those functions or products, i. e., the ultimate sexual effects of temperature acting upon the immature stages or upon the adults. Eidmann (*7*) found that when lepidopterous pupae were placed at a low temperature (unstated), the emerged adults produced fewer eggs; and Pospelov (cited by Uvarov (*30*)) states that in most species of Lepidoptera, high temperatures do not affect the development of the ovaries. Bliss (*5, p. 852*) correlated egg production in several species of leafhoppers with the temperature the day previous to oviposition and concluded that "temperature was found to condition oviposition more by its indirect effect upon egg development than by its direct action on egg deposition." Alpatov (*2*) found that when *Drosophila* is reared at 30° C., it produces fewer eggs at 25° than does an insect reared at 19°. Data presented in table 9 indicate that the opposite effect is produced on *Trichogramma*.

By reference to table 10 it will be noted that the progeny of parasites developing at 15° C. are preponderantly male, i. e., developed from unfertilized eggs. This low sex ratio must be due to a reduced potency of the male parents reared at 15°, since the number of male progeny is consistently higher than the number of female progeny throughout the lives of the parent females, thus indicating that the females have not been properly impregnated.

TABLE 10.—*Sex ratios of the progeny of pairs reared through their immature stages at different temperatures*

| Temperature °C. | ♀/total | Total counted |
|---|---|---|
| 30 | 0.62 | 933 |
| 25 | .66 | 1,788 |
| 20 | .57 | 614 |
| 15 | .42 | 2,425 |

Peterson (*22*) and Schread and Garman (*25*) note that when parasitized *Sitrotroga* eggs are kept under certain conditions of refrigeration, a change in the sex ratio of the emerging parasites occurs. This is undoubtedly a matter of selective mortality between the sexes as was pointed out by Peterson (*22*), and not the result of an actual alteration of the germ plasm. The data in table 10, however, indicate that a real reduction in the potency of the males is effected if they are reared to maturity at low temperatures.

The longevity and productivity of parasites as affected by temperature—acting either upon the immature stages or upon the adults—are summarized graphically in figure 2.

It appears from tables 9 and 10 and from figure 2 that adults to be liberated in the field in a pest-control project should not be those emerging from host eggs which, for the purpose of retarding development, have been kept at a temperature lower than 20° C., for if

such adults are used, the lower sex ratio of their progeny, their markedly shorter life, and their reduced productivity, will reduce the probability of success. It would seem that artificial rearing at about 25° to 30° is conducive to a longer life and a greater number of eggs in the field, the greater longevity at 30° being about offset by the greater productivity at 25°. In building up populations in the laboratory, however, 30° C. is probably a more efficient rearing temperature than 25°,

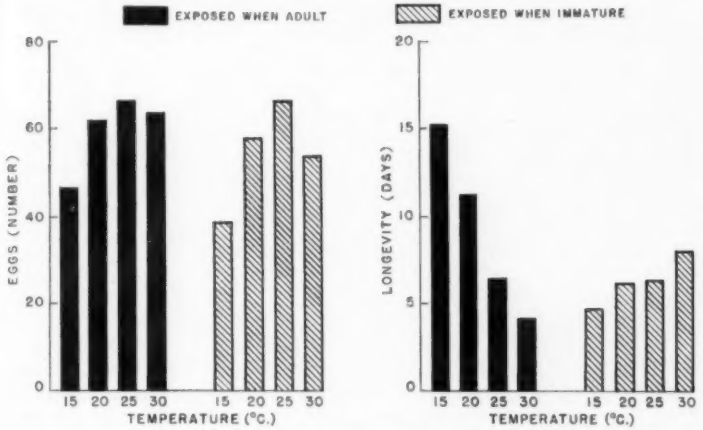


FIGURE 2.—Effects of temperature upon the productivity and female longevity of *Trichogramma*.

since the reduction in development time at 30° (about one-third less than at 25°) certainly more than offsets the advantages of higher productivity at 25°.

## EFFECTS OF MOISTURE CONDITIONS

Quantitative data on the effects of humidity upon the longevity and productivity of insects are rare and, so far as the writer is aware, no attempts have been made to differentiate between the effect of moisture upon the development of the sexual capabilities and upon the process of oviposition itself. Certainly nothing of this sort has been done for *Trichogramma*.

### EFFECTS OF HUMIDITY ACTING UPON THE ADULTS

In these experiments, the parasites were reared to maturity at the standard condition of 25° C. and 5-mm saturation deficiency, and immediately after emergence were fed, paired, and placed at atmospheric conditions of 0-mm (saturation), 5-mm, 10-mm and 15-mm saturation deficiency. In table 11 the longevity and productivity at these successively drier conditions are compared.

It will be noticed that at a saturation deficiency of 10 and 15 mm the longevity of both males and females is markedly reduced. Since the products of the saturation deficiencies (governing rate of evaporation) and the longevities (duration of evaporation) at 10 and 15 mm are about equal (43.0 and 45.0 respectively for the females and 44.0 and 36.0 for the males) the total amounts of water evaporated from the

parasites at these two conditions were about equal. This would indicate that in these cases the limiting lethal factor is probably desiccation and that the desiccation limit is around 40 mm—days.

TABLE 11.—*Productivity (black host eggs) and longevity of pairs spending their adult lives at different moisture conditions*

| Treatment and factors observed [1] | N | Mean±S. E. | Difference± S. E. | Difference / S. E. difference |
|---|---|---|---|---|
| 0 mm (saturation): | | | | |
| Progeny.....number.. | 46 | 64.0±1.7 | | |
| ♀ longevity.....days.. | 46 | 6.8± .3 | | |
| ♂ longevity.....do..... | 44 | 5.2± .2 | | |
| 5 mm: | | | | |
| Progeny.....number.. | 70 | 66.1±2.5 | [2]−2.1±3.0 | 0.7 |
| ♀ longevity.....days.. | 71 | 6.3± .3 | [2].5± .4 | 1.2 |
| ♂ longevity.....do..... | 63 | 5.7± .2 | [2]−.5± .3 | 1.7 |
| 10 mm: | | | | |
| Progeny.....number.. | 57 | 58.4±2.0 | [3]7.7±3.2 | 2.4 |
| ♀ longevity.....days.. | 57 | 4.3± .3 | [3]2.0± .4 | 5.0 |
| ♂ longevity.....do..... | 58 | 4.4± .1 | [3]1.3± .2 | 6.5 |
| 15 mm: | | | | |
| Progeny.....number.. | 58 | 51.9±1.2 | [4]6.5±2.3 | 2.8 |
| ♀ longevity.....days.. | 58 | 3.1± .2 | [4]1.2± .4 | 3.0 |
| ♂ longevity.....do..... | 58 | 2.4± .1 | [4]2.0± .1 | 20.0 |

[1] Temperature 25° C.; saturation deficiencies in millimeters of mercury.
[2] 0 mm minus 5 mm.
[3] 5 mm minus 10 mm.
[4] 10 mm minus 15 mm.

Since death in a saturated atmosphere must be due to other causes than desiccation, and since the longevity is about equal at saturation and at 5-mm saturation deficiency, death in the latter case also must be due to other causes than desiccation. In other words, the adult parasites are able to live out their normal span of life at about 5-mm saturation deficiency or lower, but at 10-mm or higher the longevity is markedly reduced as a result of the drying effect of the atmosphere. It will be noticed, though, that the effects upon productivity are much less pronounced than the effects upon longevity. This is to be expected since, due to the characteristically high initial egg production by *Trichogramma*, the detrimental effects of high water loss should not be reflected in the reduced oviposition of the female until most of her eggs have already been laid.

The general nature of the egg-laying curve is about the same at the various moisture conditions as at the standard condition (see fig. 1), a more rapid termination as a result of a shorter life at 10- and 15-mm saturation deficiency being the only apparent difference.

The sex ratio of the progeny is reduced as the humidity is lowered (table 12). This reduction is apparently due to the reduced initial copulation activity of the males at low humidities, since after the first laying period the sex ratio abruptly returns to normal.

TABLE 12.—*Sex ratios of progeny of pairs kept at various humidity conditions*

| Saturation deficiency (mm Hg) | Females total | Total counted |
|---|---|---|
| 0 | 0.57 | 2,310 |
| 5 | .66 | 1,788 |
| 10 | .44 | 2,476 |
| 15 | .39 | 2,200 |

The data in tables 11 and 12 on adults placed at four different humidity conditions, suggest that field liberations can be made to best advantage when the saturation deficiency is 5 mm or less, i. e., when the relative humidity is above 84.3 percent at 30° C., 78.8 percent at 25°, or 71.6 percent at 20°.

In building up laboratory stocks, where longevity is not of much importance, since host eggs are usually presented to the parasites shortly after their emergence, any saturation deficiency less than about 10 mm, i. e., relative humidities above 68.6 percent at 30° C., 57.0 percent at 25°, or 43.0 percent at 20°, should be satisfactory.

### Effects of Humidity Acting Upon the Immature Stages

In these experiments, the parasites were reared to maturity at 25° C. in atmospheres of 0-mm (saturation), 5-mm, and 15-mm saturation deficiency. Within 12 hours after emergence all adult parasites were fed, paired, and placed at the standard condition where they remained for the rest of their lives. Thus the influence of high and low humidities upon the development of the sexual structures and products was tested at the single condition. The results of these experiments are presented in table 13.

Table 13.—*Productivity (black host eggs) and longevity at 5-mm saturation deficiency of pairs reared to maturity at 0-mm, at 5-mm, and at 15-mm saturation deficiency*

| Treatment and factors observed [1] | N | Mean±S. E. | Difference± S. E. | Difference / S. E. difference |
|---|---|---|---|---|
| 0 mm (saturation): | | | | |
| Progeny.....number.. | 63 | 59.1±2.5 | ..... | ..... |
| ♀ longevity.....days.. | 63 | 6.0± .3 | ..... | ..... |
| ♂ longevity.....do.... | 65 | 5.7± .1 | ..... | ..... |
| 5 mm: | | | | |
| Progeny.....number.. | 70 | 66.1±2.5 | [2] −7.0±3.5 | 2.0 |
| ♀ longevity.....days.. | 71 | 6.3± .3 | [2] −.3± .4 | .7 |
| ♂ longevity.....do.... | 63 | 5.7± .2 | [2] .0± .2 | .0 |
| 15 mm: | | | | |
| Progeny.....number.. | 43 | 40.3±2.0 | [3] 25.8±3.2 | 8.1 |
| ♀ longevity.....days.. | 39 | 5.7± .3 | [3] .6± .4 | 1.5 |
| ♂ longevity.....do.... | 45 | 5.5± .3 | [3] .2± .4 | .5 |

[1] Temperature 25° C.; saturation deficiencies in millimeters of mercury.
[2] 0 mm minus 5 mm.
[3] 5 mm minus 15 mm.

It will be seen that the humidity in which the parasites are reared to maturity has no effect upon the longevity of the subsequent adults, but both higher and lower humidities (saturation and 15-mm saturation deficiency) reduce the productivity.

The sex ratios of the progeny produced are not significantly affected by the moisture conditions at which the parents are reared to adulthood. At saturation the ratio of females to the total number of progeny counted was 0.55 (2,930 counted), whereas at 15-mm saturation deficiency the ratio was 0.63 (1,266 counted).

In figure 3 the data on the influence of atmospheric moisture upon the longevity and productivity of *Trichogramma* are summarized graphically.

It will be seen that humidity has the same general influence upon egg production when it acts upon the developmental stages as when it acts upon the adults only. The effects are much more pronounced, how-

ever, when the influence is exerted on the immature stages. In other words, the effects of adverse moisture conditions are more pronounced when they act during the relatively long developmental period (about 10 days) than when they influence directly the function of oviposition during the short adult life, only the very first part of which is of much significance in the total productivity.

On the other hand, the longevity of adult parasites exposed as adults is much more markedly affected by atmospheric humidity than is the

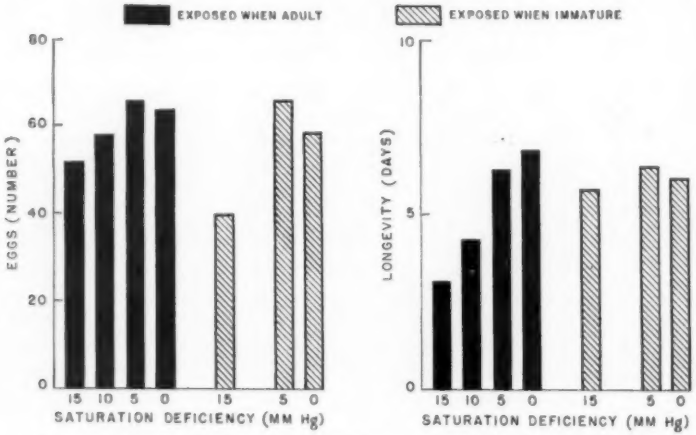


FIGURE 3.—Effects of humidity upon productivity and female longevity of *Trichogramma*.

longevity of adults exposed as eggs, larvae, and pupae. Apparently the influence of moisture during development is exerted more or less specifically upon the reproductive function and not on the general factors that determine length of life.

These data suggest that in building up both laboratory stocks and stocks for field liberation, the ideal atmospheric humidity in which to rear the parasites to maturity is within 5 mm of saturation.

## SUMMARY AND CONCLUSIONS

The longevity and productivity of *Trichogramma evanescens* Westwood, reared in *Sitotroga* eggs, were tested under various conditions of feeding, withholding host eggs, pairing, superparasitism, light, temperature, and humidity. From the experimental data, the following results were obtained and conclusions drawn:

(1) The average number of progeny produced at 25° C. and 5-mm saturation deficiency is $66.1 \pm 2.5$, the female longevity $6.3 \pm 0.3$ days, the male longevity $5.7 \pm 0.2$ days, and the sex ratio 0.66 female.

(2) A correlation of $+0.639 \pm 0.071$ exists between the longevity of mated females and their productivity.

(3) Since females fed on dilute honey live longer and produce more progeny than unfed females, parasites should be fed before liberation in the field.

(4) Females live longer when host eggs are present than when they are absent, but if the eggs are withheld for 48 or 72 hours, female longevity is unaffected while productivity is reduced. Therefore only young parasites should be liberated in the field.

(5) Pairing reduces productivity but leaves longevity unaffected.

(6) Females emerging from superparasitized host eggs produce fewer progeny than normal females but live as long. Males reared under the same conditions, while sexually potent, are shorter-lived than normal males.

(7) Females kept in diffused light live slightly longer, than females kept in total darkness, but produce the same number of progeny.

(8) Adult longevity varies inversely as the temperature to which the adults are subjected, but directly as the temperature to which their developmental stages are exposed; the optimum temperature for productivity is about 25° C. in either case. These facts suggest that the most favorable field temperature at which to liberate the parasites for pest control is probably just under 25°, whereas the most favorable laboratory breeding temperature is about 30°.

(9) An abnormally high proportion of male progeny is produced by parasites developing at 15° C. (only 0.42 female).

(10) When adults are subjected to either low (10-mm or 15-mm saturation deficiency) or high (saturation) humidities, their productivity is somewhat reduced, but relatively less so than their longevity, and the total water lost before death is about the same at both "dry" conditions; but, conversely, when the immature stages are exposed to low or high humidities, the productivity of the subsequently emerging adults is decidedly reduced while the longevity is unaffected. The most favorable field humidity at which to liberate the parasites would appear to be 5-mm saturation deficiency or less, but laboratory breeding conditions of 10-mm saturation deficiency or less are probably satisfactory.

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# MEIOTIC INSTABILITY AS AN INHERITED CHARACTER IN VARIETIES OF TRITICUM AESTIVUM [1]

By W. M. MYERS, *instructor in plant genetics, Minnesota Agricultural Experiment Station*, and LEROY POWERS, *senior geneticist, Division of Fruit and Vegetable Crops and Diseases, Bureau of Plant Industry, United States Department of Agriculture*

## INTRODUCTION

In previous studies of varieties of *Triticum aestivum* L., Powers (*16, 17, 18*)[2] found that the cytological aberrations of nonorientation of the chromosomes in meiosis, the occcurence of univalents at metaphase, and chromatin loss in the parent plants were associated with the coefficients of variability of their progeny for weight of seed per plant, height of plant, and percentage of fruitfulness. These results indicated that in some cases meiotic instability is an important character in a breeding program. For this reason it seemed desirable to study the relative importance of heredity and environment in the determination and differentiation of this character.

## MATERIALS AND METHODS

The frequency of occurrence of chromatin loss was employed as a measure of meiotic instability. The reasons for using this character were twofold. (1) Chromatin loss was found to be highly correlated with nonorientation and the occurrence of univalents (*17, 18*). Thus of the single determinations, it seemed best adapted as a criterion of meiotic instability. (2) It permitted the collection of data on a larger number of plants than would have been possible if a number of meiotic irregularities had been studied. To determine chromatin loss, 500 immature microspores, still in the form of quartets, were examined for each plant and the number showing micronuclei was recorded.

Five varieties of *Tritucum aestivum*, namely, Marquis, Supreme, Thatcher, Double Cross 2305, and H–44, were selected for use in this study. Marquis and Thatcher were included because in previous investigations (*17, 18*) both of these varieties were found to be comparatively free from meiotic instability. In preliminary studies, Double Cross 2305 and H–44 had shown a fairly high degree of meiotic instability while Supreme was known to be variable in many agronomic characters and it seemed, therefore, that this variety might also be meiotically unstable.

Plants of the five varieties were studied cytologically in 1931. In 1932, 1933, and 1936, progeny rows were grown from various selections and in all cases from seed produced under bag to insure self-pollination. Plants having a low percentage of micronuclei were selected in 1931 from Thatcher, Marquis, Double Cross 2305, and H–44; plants having a high percentage of micronuclei were selected from Double Cross

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[2] Reference is made by number (italic) to Literature Cited, p. 451.

2305 and H–44; and a plant intermediate between low and high was selected from Marquis. The individual plant selections in 1931 and their progeny in later generations will be designated as lines. The progenies of these eight lines were studied cytologically in 1932. In 1933 each line was the progeny of a randomly selected individual plant of 1932 and, in 1936, individual progenies of from 7 to 10 plants of each line were studied. Thus conclusions drawn from the study on the inheritance of meiotic instability are based on 3 years of progeny testing.

The histories of the different varieties are of value in interpreting the results and therefore are given here. Marquis resulted from a cross of two aestivum varieties and Supreme was produced by selection from Red Bobs, an aestivum variety. Thatcher originated from a cross of a selection of Marquis × Iumillo (a variety of *Triticum durum*) with a selection from Kanred × Marquis, (*13*) and Double Cross 2305 was a sister selection of Thatcher. H–44 was produced by McFadden (*15*) from a cross between Yaroslav emmer and Marquis.

For the first 3 years of the test, the effects of the environment, if any, could not be separated from possible genetic effects. Therefore, in order to collect information regarding environmental effects, a more intensive study including different dates of collecting the cytological material was set up for 1936.

For the cytological studies, part of the material was killed and fixed in Allen's modification of Bouin's fixative and the slides were stained by Newton's iodine gentian-violet method described by LaCour (*14*). For the majority of the studies, Belling's (*9*) iron aceto-carmine smear method was used, the material having been killed and fixed in acetic alcohol (3 parts of absolute alcohol : 1 part of glacial acetic acid) and stored in 70-percent alcohol.

## EXPERIMENTAL RESULTS

### INHERITANCE OF MEIOTIC INSTABILITY

The data having a bearing on the inheritance of meiotic instability were evaluated under the following classifications, the percentage of micronuclei for the varieties from which the lines used in this study were selected, 3 years of progeny testing, homozygosity of lines and cultures, and the number of monosomic plants obtained from each line and variety.

The frequency distributions of percentage of micronuclei for the varieties from which the lines used in this study were established are given in table 1.

The five varieties occurred in three distinct groups on the basis of percentage of micronuclei. No plants were found in either Thatcher or Marquis with more than 3 percent of micronuclei while none of the plants of Supreme had less than 3 percent. The plants of H–44 and D. C. 2305 ranged from less than 1 percent to more than 19 percent of micronuclei. One plant of each of these two varieties and four plants of Supreme showed more than 19 percent of mironuclei. Metaphase and anaphase I studies of these plants revealed that each was monosomic, having only 41 somatic chromosomes. These results agree with those reported by Powers (*17*) for monosomic plants of *Triticum aestivum*. Since the high percentage of micronuclei of monosomic

plants is due largely to the loss of the univalent chromosome, these plants have not been included in the averages for the varieties. That differences between the varieties were statistically significant can be seen from the data given at the bottom of table 1. Likewise, the monosomic plants were not included in these calculations. If these differences are characteristic of certain varieties and strains, it is evident that they are inherited. To determine whether characteristic differences do occur, progeny tests were conducted for 3 years.

TABLE 1.—*Frequency distribution of percentage of micronuclei for the varieties from which the lines used in this study were established, and analysis of variance to determine whether the differences between varieties could be due to the errors of random sampling*

FREQUENCY DISTRIBUTION

| Variety | Total plants | Plants with the indicated percentage of micronuclei | | | | | Mean percentage of micronuclei |
|---|---|---|---|---|---|---|---|
| | | 0–1.0 | 1.1–3.0 | 3.1–10.0 | 10.1–19.0 | 19.1–26.0 | |
| | *Number* | *Number* | *Number* | *Number* | *Number* | *Number* | *Percent* |
| Thatcher | 25 | 18 | 7 | | | | 0.8 |
| Marquis | 26 | 17 | 9 | | | | .9 |
| H–44 | 20 | 4 | 6 | 7 | 2 | 1 | 4.1 |
| D. C. 2305 | 11 | 4 | 1 | 2 | 3 | 1 | 5.5 |
| Supreme | 9 | | | 4 | 1 | 4 | 8.3 |

ANALYSIS OF VARIANCE

| Variance | *D. F.* | Mean square | *F* | Value of *F* for a *P* of 0.01 |
|---|---|---|---|---|
| Between varieties | 4 | 201.436 | 51.21 | 3.56 |
| Within varieties | 80 | 3.934 | | |

The data collected in the three generations of progeny testing are given in table 2. These data were analyzed to determine whether the differences could be accounted for by the errors of random sampling.

TABLE 2.—*Yearly average percentage of micronuclei for each line, number of plants making up the averages, and the analysis of variance for each year*

PERCENTAGE OF MICRONUCLEI AND NUMBER OF PLANTS

| Line | Average percentage of micronuclei for— | | | | | | Plants making up the yearly averages | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1931 | 1932 | 1933 | 1936 | 1931–33 | 1931–36 | 1931 | 1932 | 1933 | 1936 |
| | *Percent* | *Percent* | *Percent* | *Percent* | *Percent* | *Percent* | *Number* | *Number* | *Number* | *Number* |
| Thatcher-L | 0.3 | 1.1 | 0.6 | 1.6 | 0.67 | 0.90 | 1 | 10 | 7 | 51 |
| Marquis-L | .5 | .5 | 1.3 | 1.4 | .77 | .92 | 1 | 10 | 10 | 53 |
| Marquis-M | 2.2 | 3.3 | 3.0 | 3.3 | 2.83 | 2.95 | 1 | 10 | 10 | 58 |
| D. C. 2305-L | .7 | .7 | 2.2 | | 1.20 | | 1 | 3 | 8 | |
| D. C. 2305-M | 15.6 | .8 | 3.1 | | 6.50 | | 1 | 8 | 8 | |
| H–44-L | .7 | 2.1 | 1.8 | | 1.53 | | 1 | 10 | 8 | |
| H–44-M | 13.3 | 3.2 | 3.2 | 3.3 | 6.57 | 5.60 | 1 | 1 | 10 | 40 |
| H–44-H | 13.0 | 4.8 | 12.3 | 5.2 | 10.03 | 8.82 | 1 | 10 | 7 | 42 |

TABLE 2.—*Yearly average percentage of micronuclei for each line, number of plants making up the averages, and the analysis of variance for each year*—Contd.

ANALYSIS OF VARIANCE

| Year | D. F. | | Mean square | | F | Value of F for a P of 0.01 [1] |
|---|---|---|---|---|---|---|
| | Between lines | Within lines | Between lines | Within lines | | |
| 1931 [2] | 4 | 80 | 201.4358 | 3.9336 | 51.21 | 3.56 |
| 1932 | 6 | 54 | 42.1162 | 3.3995 | 12.39 | 3.19 |
| 1933 | 7 | 60 | 98.1947 | 5.3638 | 18.31 | 2.97 |
| 1936 | 4 | 247 | 115.3965 | 6.4470 | 17.90 | 3.41 |

[1] The values of $F$ for $P$ of 0.01 are for the nearest degrees of freedom given by Snedecor (*20*).
[2] For 1931 the analysis given is for "between varieties" and "within varieties."

Since several progenies were grown for each line in 1936 under randomization, the mean square within lines seems reliable as an error in obtaining the $F$ value. It was used also in the other years. For every generation as represented by years, the $F$ value was considerably larger than that necessary to give a $P$ of 0.01. It may be concluded that for every generation some of the differences between lines were too great to be attributed to the errors of random sampling and therefore some of the differences may be judged statistically significant.

To determine which differences between the lines selected for high and low meiotic instability may be judged statistically significant, the standard error of the difference was used. The differences between the high and low selections divided by the standard error of their differences are given in table 3.

TABLE 3.—*Differences between lines divided by their standard error*

| Lines compared | Difference divided by the standard error | | |
|---|---|---|---|
| | 1932 | 1933 | 1936 |
| Marquis-L with Marquis-M | −3.40 | −1.60 | −4.00 |
| Double Cross 2305-M with D. C. 2305-H | −.08 | −.80 | |
| H-44-L with H-44-M | −.60 | −1.30 | |
| H-44-M with H-44-H | −.80 | −7.80 | −3.40 |
| H-44-L with H-44-H | −3.30 | −8.80 | |

The high values for the difference divided by the standard error leaves little room for questioning that the lines within Marquis differ significantly and that H–44–M and H–44–L are significantly different from H–44–H.

The most critical evidence on the inheritance of meiotic instability is furnished by the sign (plus or minus) of the difference. In table 3 the minus signs indicate that the differences were all negative. The negative values indicate that the lines selected for low meiotic instability were uniformly lower in percentage of micronuclei than the lines from parents of higher variability. Thus, these data are rather conclusive in showing that meiotic instability is inherited.

The material of the five lines studied in 1936 consisted of the progenies of 42 plants. The percentage of micronuclei of 38 of these 42

plants was determined in 1933. The correlation coefficient for percentage of micronuclei of the 38 plants with the average percentage of micronuclei of their progenies in 1936 was 0.77, a highly significant value. This lends further support to the conclusion that heritable differences in meiotic instability existed.

In 1936 the experiment was designed to yield some information regarding the nature of the inheritance of meiotic instability. In this regard, it was of interest to know whether homozygous lines, significantly different in percentage of micronuclei, had been obtained. The data having a bearing on this problem are given in table 4.

TABLE 4.—*Homozygosity of lines in 1936 for percentage of micronuclei as determined by the analysis of variance*

| Lines | *D. F.* for— | | Mean square for— | | *F* | Value of *F* for a *P* of [1]— | |
|---|---|---|---|---|---|---|---|
| | Cultures | Error | Cultures | Error | | 0.05 | 0.01 |
| Thatcher | 8 | [2] 37 | 3.449 | 3.246 | 1.06 | 2.22 | 3.07 |
| Marquis–L | 8 | [3] 39 | 5.250 | 2.555 | 2.05 | 2.18 | 2.99 |
| Marquis–M | 9 | [4] 43 | 5.882 | 1.686 | 3.49 | 2.18 | 2.99 |
| H–44–M | 6 | [4] 28 | .066 | 2.338 | | | |
| H–44–H | 6 | 30 | 62.073 | 11.286 | 5.50 | 2.42 | 3.47 |

[1] The values of *F* for *P* values of 0.05 and 0.01 are those values for the nearest degrees of freedom given by Snedecor (*20*).
[2] 3 values missing and interpolated.
[3] 1 value missing and interpolated.
[4] 2 values missing and interpolated.

Microsporocytes were collected from one plant of each culture on each of 6 days from June 22 to June 27, inclusive. The material was not at the proper stage for determining the percentage of micronuclei in two plants each of Marquis–M and H–44–M and three plants of Thatcher. In addition, one plant of Marquis–L was monosomic and therefore was omitted from the calculation. In calculating the analysis of variance, values for these plants were interpolated, using the formula given by Yates (*21*).

From the *F* values in table 4, it would seem that Thatcher and H–44–M are homozygous for percentage of micronuclei. The *F* value for Marquis–L almost reaches that expected for a *P* of 0.05 and the *F* value for Marquis–M exceeds the value of F for a *P* of 0.01. These results indicate that the last two lines are not homozygous for percentage of micronuclei. However, such a conclusion is difficult to justify from an examination of table 2. As shown by the mean percentage of micronuclei for years, the progeny test for Marquis–L would lead one to suspect that this line was as stable as Thatcher and therefore homozygous. Likewise, uniformity of the mean percentage of micronuclei for Marquis–M in different years was striking and certainly would lead one to believe that this line was homozygous for the character in question.

Since the data indicate that Thatcher and H–44–M are homozygous, it is desirable to know whether the difference between these two lines can be accounted for by the errors of random sampling. From table 5 it can be seen that the odds against the differences between the means of these two lines being due to the errors of random sampling are very large.

TABLE 5.—*Comparison of the mean percentage of micronuclei of the 5 lines studied in 1936 by means of the standard error of the difference*

| Comparison | Difference | D/S. E. | Comparison | Difference | D/S. E. |
|---|---|---|---|---|---|
| Thatcher with Marquis-L | 0.2 | 0.4 | Marquis-L with H-44-M | 1.9 | 3.6 |
| Thatcher with Marquis-M | 1.7 | 3.6 | Marquis-L with H-44-H | 3.8 | 7.3 |
| Thatcher with H-44-M | 1.7 | 3.2 | Marquis-M with H-44-M | .0 | .0 |
| Thatcher with H-44-H | 3.6 | 6.9 | Marquis-M with H-44-H | 1.9 | 3.7 |
| Marquis-L with Marquis-M | 1.9 | 4.0 | H-44-M with H-44-H | 1.9 | 3.4 |

The variation of plants of H–44–H in percentage of micronuclei in 1933 indicated that this line was not breeding true for this character. This was substantiated by the behavior of the progenies of these plants in 1936 (table 4).

To determine whether any of the plants of H–44–H studied in 1933 were homozygous for factors determining meiotic instability, a more extensive study of their progenies in 1936 was made. Material was collected from all of the available plants of the seven cultures of H–44–H and data on percentage of micronuclei were obtained for a total of 129 plants. These data are summarized in table 6.

TABLE 6.—*Number of plants, frequency distribution of plants in each line for percentage of micronuclei, and average percentage of micronuclei for cultures of H–44–H in 1936*

| Culture No. | Plants studied | Plants showing indicated percentage of micronuclei | | | | | Average percentage of micronuclei |
|---|---|---|---|---|---|---|---|
| | | 0–1.0 | 1.1–3.0 | 3.1–10.0 | 10.1–19.0 | 19.1–26.0 | |
| | *Number* | *Number* | *Number* | *Number* | *Number* | *Number* | *Percent* |
| C38 | 17 | 1 | 5 | 8 | 3 | | 6.9 |
| C9 | 20 | 3 | 4 | 7 | 4 | 2 | 6.1 |
| C19 | 18 | 1 | 6 | 6 | 3 | 2 | 6.0 |
| C5 | 21 | 2 | 9 | 6 | 4 | | 4.7 |
| C18 | 21 | 5 | 5 | 8 | 3 | | 4.5 |
| C22 | 13 | 4 | 5 | 4 | | | 2.8 |
| C4 | 19 | 5 | 11 | 1 | | 2 | 1.7 |

Six of the 129 plants had more than 19 percent of micronuclei. The chromosome number of three of these plants, namely, the two occurring in culture No. 4 and one in culture No. 19, was determined and each plant was found to be monosomic. It seems probable that the other three plants may also have been monosomic since the percentage of micronuclei shown by each is within the range for monosomic plants. For this reason, these six plants were not included in the calculation of the means for the cultures.

Five of the seven cultures of H–44–H had plants with less than 1 and more than 10 percent of micronuclei while, in the remaining two cultures, all plants with 42 chromosomes showed less than 10 percent of micronuclei. This range in percentage of micronuclei of the different plants indicated that the seven cultures were still segregating for meiotic instability. Since the 500 microspores of each plant were counted in groups of 100, it was possible to measure the variation within plants and determine whether significant differences between plants existed. For this purpose an analysis of variance was calculated for each culture (table 7).

TABLE 7.—*Summary of the analysis of variance of percentage of micronuclei for each culture of H–44–H grown in 1936*

| Culture No. | *D. F.* | | Mean square | | *F* | Value of *F* for *P* of—[1] | |
|---|---|---|---|---|---|---|---|
| | Between plants | Within plants | Between plants | Within plants | | 0.05 | 0.01 |
| C38 | 16 | 68 | 147.1280 | 10.7058 | 13.74 | 1.89 | 2.45 |
| C9 | 17 | 72 | 161.5350 | 8.5833 | 18.82 | 1.89 | 2.45 |
| C19 | 15 | 64 | 145.8133 | 9.2312 | 15.80 | 1.89 | 2.45 |
| C5 | 20 | 84 | 91.0295 | 7.0520 | 12.91 | 1.65 | 2.03 |
| C18 | 20 | 84 | 105.2314 | 7.9000 | 13.32 | 1.65 | 2.03 |
| C22 | 12 | 52 | 31.3718 | 4.1077 | 7.64 | 1.95 | 2.56 |
| C4 | 16 | 68 | 5.1941 | 2.4882 | 2.09 | 1.89 | 2.45 |

[1] Values for nearest degrees of freedom given by Snedecor (*20*).

For six of the cultures the value of *F* for comparing mean square between plants with mean square within plants was greater than *F* for a *P* of 0.01. In culture 4, the value of *F* gave *P* between 0.05 and 0.01. Therefore, it appears that none of these lines was homozygous for meiotic instability.

The number of monosomic plants obtained from each line and the total number from each variety together with the mean percentage of micronuclei are shown in table 8.

TABLE 8.—*The number of monosomic plants obtained from each line and variety*

| Line or variety | Total plants | Monosomic plants | Mean percentage of micronuclei | Line or variety | Total plants | Monosomic plants | Mean percentage of micronuclei |
|---|---|---|---|---|---|---|---|
| | *Number* | *Number* | *Percent* | | *Number* | *Number* | *Percent* |
| Thatcher | 93 | 0 | 0.90 | H–44–L | 18 | 0 | 1.53 |
| Marquis–L | 73 | 1 | .92 | H–44–M | 51 | 0 | 5.60 |
| Marquis–M | 78 | 0 | 2.95 | H–44–H | 129 | [1] 6 | 8.82 |
| Total [2] | 177 | 1 | | Total [2] | 218 | 7 | |
| D. C. 2305–L | 11 | 0 | 1.20 | Supreme | 9 | 4 | 8.30 |
| D. C. 2305–M | 16 | 0 | 6.50 | | | | |
| Total [2] | 38 | 1 | | | | | |

[1] 3 of these plants were determined to be monosomic on the basis of the percentage of micronuclei.
[2] Total for the variety includes data for 1931 before the lines within the varieties were established.

It is evident that in this investigation the varieties showing the highest percentage of micronuclei tended to have the greater number of monosomic plants. Since monosomic plants arise from chromatin loss such an association would be expected. Thus, lines exhibiting a high degree of meiotic instability are rendered even more unstable by the occurrence of these monosomic plants. An occasional monosomic plant among the progeny of such meiotically stable varieties as Thatcher and Marquis would be expected. One such plant was found in Marquis.

### THE EFFECT OF THE ENVIRONMENT ON MEIOTIC INSTABILITY

The data on the effect of environment upon meiotic instability are given in table 9.

TABLE 9.—*The average percentage of micronuclei of each line for each of the 6 days of collection in 1936*

| Line or variety | Average percentage of micronuclei for— | | | | | |
|---|---|---|---|---|---|---|
| | June 22 | June 23 | June 24 | June 25 | June 26 | June 27 |
| | *Percent* | *Percent* | *Percent* | *Percent* | *Percent* | *Percent* |
| Thatcher | 0.8 | 0.9 | 0.6 | 2.4 | 2.1 | 2.5 |
| Marquis–L | .5 | .9 | 1.1 | 1.8 | 1.8 | 1.8 |
| Marquis–M | 2.8 | 3.0 | 2.8 | 3.7 | 4.2 | 3.8 |
| H–44–M | 2.5 | 1.4 | 1.8 | 4.1 | 3.1 | 6.9 |
| H–44–H | 2.1 | 4.9 | 3.5 | 6.3 | 8.7 | 5.7 |
| Average | 1.7 | 2.2 | 2.0 | 3.7 | 4.0 | 4.1 |

Microsporocytes were collected from one plant of each culture on each of 6 days in 1936. There was a marked difference between the percentage of micronuclei for the first 3 days and the last 3 days of collection. For purposes of evaluation it is necessary to know whether the differences noted could be attributed to the errors of random sampling. If they are due to the errors of random sampling, the probability is 0.5 that any value of a given line for the last 3 days will exceed any value of the same line for the first 3 days. Then the probability of this same value exceeding all three values for the first 3 days is $(0.5)^3$ and likewise the probability of all three values of the last 3 days for any one line exceeding all three values for the first 3 days for the same line is $(0.5)^3\ (0.5)^3\ (0.5)^3$. Completing these calculations it is seen that the odds are 499:1 against such a result occurring due to the errors of random sampling. Since the values for the last 3 days of collection of each line exceeded the value of the first 3 days of collection for the same line, it is evident that the material collected the first 3 days is significantly lower in percentage of micronuclei than that collected the last 3 days of the investigation. From this it may be concluded that environmental conditions prior to the collection of the material are a factor in determining the percentage of micronuclei that a given plant possesses.

## DISCUSSION

One of the major advances in the development of superior varieties of aestivum wheat was the transfer of the field resistance to black stem rust of varieties of the emmer and durum group to bread wheat varieties. Marquillo, developed at the Minnesota Agricultural Experiment Station from a cross of Iumillo durum with Marquis, and Hope and H–44, developed from a cross of Yaroslav emmer × Marquis made by McFadden (*15*), are notable examples of aestivum varieties which have received genes for rust resistance from varieties of the emmer and durum group. Two of these varieties, Marquillo and H-44, have been investigated cytologically and found to be significantly more irregular in meiosis than the standard variety, Marquis (Powers (*16*, *17*, *18*) and the present investigations). Although it cannot be concluded from these two cases that varieties produced by interspecific hybridization will all show meiotic instability, selections produced in this manner should be investigated cytologically because of the possibility that they might exhibit such variability.

The results obtained with Supreme indicate that meiotic irregularity is not confined to selections from interspecific hybrids. As stated previously, Supreme was produced by selection from Red Bobs, an aestivum variety. Yet Supreme was found to be even more unstable in 1931 than H–44. The possibility that Supreme may have arisen as a result of natural crossing must of course not be overlooked.

The cytological behavior of Thatcher and D. C. 2305 is of considerable interest. These varieties are sister selections from the double cross (Iumillo × Marquis) × (Kanred × Marquis) and both show the same type of rust resistance as their (Iumillo × Marqius) parent. Thatcher was at least as stable cytologically as Marquis while D. C. 2305 showed a significantly higher degree of meiotic instability. These results indicate that although selections obtained from hybrids between species may be unstable, cytologically stable varieties having the desirable characteristics obtained from the related species may be produced by crossing with a variety which does not show meiotic irregularities.

The investigations reported in this paper show that differences in meiotic instability are conditioned to a considerable extent at least by heritable factors. The variation between plants of the same variety suggested the possibility of selection of stable lines even from such varieties as H–44. The different lines obtained from Marquis and H–44 indicate that selection has been effective in isolating types that differ significantly in cytological behavior. In these investigations, selection was practiced only in 1931. It is possible that by continued selection of plants showing a low percentage of micronuclei, even more stable lines than those obtained in this study might be isolated. This possibility should be investigated.

The design of the experiment in 1936 was such that some information could be derived from the data obtained regarding the nature of the heritable differences conditioning differences in meiotic instability. The meiotic irregularities might arise from genetic factors which govern chromosome behavior, from structural differences between synapsing chromosomes or perhaps from similarities between chromosomes of different genomes which would lead occasionally to the formation of trivalents or quadrivalents at metaphase I. If the occurrence of micronuclei is to be accounted for by structural differences between synapsing chromosomes, inbreeding should tend to eliminate these differences and all homozygous lines should be fluctuating about the same mean percentage of micronuclei. Actually, apparently homozygous lines, differing significantly in percentage of chromatin loss, were obtained. The mean percentages of micronuclei of Thatcher, Marquis–L, Marquis–M, and H–44–M remained relatively constant during the 3 years of progeny testing whereas the elimination of structural differences due to inbreeding should cause a decrease in chromatin loss.

That the differences in meiotic instability could be accounted for by similarity between chromosomes of different genomes likewise seems improbable. The occurrence of occasional multivalent associations, reported by Powers (*17*) and other workers, indicates that partial homology does exist between chromosomes of different genomes. Such partial homology, in the absence of structural differences between

members of the two respective homologous pairs, should lead to the formation of quadrivalents instead of trivalents and univalents in a majority of cases. The writers do not know of any evidence that quadrivalents lead to chromatin loss. On the contrary, the senior writer (unpublished data) has investigated the occurrence of chromatin loss in *Arrhenatherum elatius* (L.) Mert. and Koch and a tetraploid strain of *Agropyron cristatum* (L.) Beauv., both of which behave cytologically like autotetraploids and in both of which seven quadrivalents per microsporocyte occasionally occur. In five plants of *A. elatius*, the percentage of micronuclei varied from 1.0 to 6.8 while in six plants of *A. cristatum* the percentage of micronuclei varied from 0.0 to 3.0 In *Triticum aestivum*, Powers (*17*) found that the correlation between the occurrence of multivalents and percentage of micronuclei was not statistically significant and that the frequency of trivalents was not great enough to account for the number of univalents found at metaphase I. In addition, Powers (*17*) found that nonorientation of bivalents at metaphase I was highly correlated with the occurrence of micronuclei and it is difficult to account for failure of bivalents to orient on the equatorial plate either on the basis of structural differences between synapsing chromosomes or partial homology of chromosomes of different genomes. Thus, the results indicate that genetic factors were involved in determining differences in percentage of chromatin loss in this study. Genetic factors affecting meiosis have been reported in maize by Beadle (*1*, *2*, *3*, *4*, *5*, *6*, *7*) and Beadle and McClintock (*8*), in *Datura* by Bergner, Cartledge, and Blakeslee (*10*), and in wheat by Sapehin (*19*). In addition, failure of pairing which may have been conditioned by genetic factors has been reported in *Nicotiana tabacum* L. by Clausen (*11*). H–44–H was still segregating in 1933. This line was investigated more extensively in 1936 and the seven cultures were all found to be segregating for percentage of micronuclei. Culture 4, which had an average of 1.7 percent of micronuclei for 19 plants and culture 22 with a mean of 2.8 percent of micronuclei for 13 plants had a considerably lower variance between plants than the remaining five cultures. In these latter cultures, the range in percent of micronuclei between plants was as great as the range of H–44 in 1931. Thus, after 3 successive years of individual plant selection, no plants were obtained in this line which appeared to be approaching homozygosity for high meiotic irregularity. Although the data were not extensive, the failure to obtain plants homozygous for high meiotic instability suggests that structural differences of the chromosomes in addition to genetic and environmental factors may have been involved in conditioning the high percentage of chromatin loss in this line.

The effect of environment on meiotic irregularity, shown by differences between dates of collection of the cytological material, indicates that comparisons between plants collected at different dates or under different environmental conditions must be interpreted with caution. Since environmental as well as heritable factors are involved in conditioning differences in meiotic instability, experiments designed to control and properly evaluate the experimental error are as necessary in studying this character as any other quantitative character.

## SUMMARY

The occurrence of chromatin loss, measured by the percentage of immature microspores showing micronuclei, was studied in five varieties of *Triticum aestivum* L., namely Marquis, Thatcher, D. C. 2305, H–44, and Supreme.

In Marquis and Thatcher all plants had less than 3 percent of micronuclei, in D. C. 2305 and H–44 plants with less than 1 percent and more than 19 percent of micronuclei were found, and all plants of Supreme had more than 3 percent of micronuclei in 1931. The relation of these data to the origin of the varieties is discussed.

Results of 3 years of progeny tests indicated clearly that heritable differences in meiotic instability occurred.

A correlation coefficient of 0.77 between the percentage of micronuclei of 38 plants in 1933 and the average percentage of micronuclei of their progenies in 1936 was obtained.

Lines differing significantly in percentage of micronuclei were isolated by selection both in Marquis and H–44. Thatcher, Marquis–L, and H–44–M were apparently homozygous in 1936 and had 1.6, 1.4, and 3.3 percent of micronuclei, respectively. H–44–H had 5.2 percent of micronuclei in 1936 and was still segregating.

The isolation of homozygous lines, significantly different in percentage of micronuclei, indicated that genetic factors were involved in conditioning meiotic instability. The failure to isolate lines homozygous for high meiotic instability in H–44–H suggested that structural differences of the synapsing chromosomes may also have been involved.

Significant differences between dates of collection of microsporocytes in 1936 indicated that the environment may also be a factor in determining differences in meiotic irregularities.


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# QUALITY STUDIES IN THE WHEAT-BREEDING PROGRAM AT THE MINNESOTA AGRICULTURAL EXPERIMENT STATION [1]

By E. R. AUSEMUS, *associate agronomist, Division of Cereal Crops and Diseases, Bureau of Plant Industry, United States Department of Agriculture,* M. C. MARKLEY, *assistant biochemist,* C. H. BAILEY, *agricultural biochemist, Division of Agricultural Biochemistry,* and H. K. HAYES, *Chief, Division of Agronomy and Plant Genetics, Minnesota Agricultural Experiment Station*

## INTRODUCTION

In breeding for improved spring and winter wheats in Minnesota, milling and baking tests were used as an aid in selecting strains of satisfactory quality.

Rather wide crosses have been used in spring wheat breeding to obtain resistance to stem rust. This resistance was obtained originally from 14-chromosome wheats, which were of poor quality for bread-making purposes. The data collected, therefore, seem satisfactory for measuring the value of milling and baking trials in the selection of wheats for quality among diverse types.

The major purpose of the winter wheat breeding was to obtain varieties as winter hardy as Minturki but more satisfactory in milling and baking quality. Crosses between spring and winter wheats have been used for this purpose and also to obtain varieties of winter wheat resistant to stem rust. In some respects the winter wheats also were very diverse in milling and baking qualities.

When the new strains are grown first in rod-row trials no information is available regarding their milling and baking qualities. In these trials, varieties with apparent low quality have been continued in the tests for at least two consecutive seasons before they have been discarded.

The strains in the $\frac{1}{40}$-acre plot trials, for the most part, have proved of rather satisfactory quality in previous trials. Standard varieties have been included along with new strains, and in the spring wheat varietal trials the rust-resistant varieties of poor baking quality, Marquillo and Hope, have been included.

The data available seemed rather satisfactory for determining the value of milling and baking trials in the breeding program.

## PREVIOUS STUDIES OF THE INHERITANCE OF QUALITY

Examples of the early application of milling and baking tests to the testing of new varieties may be found in the reports of Hays and Boss (*7*),[2] Guthrie (*4*), and Harcourt (*5*). From a study of these earlier reports, as well as from their own breeding experiments, Humphries and Biffen (*8*) concluded that baking "strength" and "weakness"

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[2] Reference is made by number (italic) to Literature Cited, p. 464.

probably constituted a simple Mendelian pair of characters. Saunders (*11*) disagreed with this conclusion and favored the view that there was not simple inheritance of baking qualities. Biffen (*1*) presented further data to support his conclusion but later (*2*) agreed with Saunders (*12*) that strength was complex in inheritance.

After it had become generally realized that baking strength is not inherited as a unit character but is an extremely complex property, conditioned by both inherited and environmental factors, the methods for determining quality characteristics underwent a long period of development, finally evolving into the present system in which baking quality is divided into a large number of factors, such as protein content, wet-gluten content and characteristics, diastatic activity, loaf volume, grain and texture of crumb, color of crumb and of crust, smoothness of crust and shape of loaf, and many others.

Zinn (*15*) first attempted the application of statistical analysis to the individual factors comprising the baking strength of varieties of wheat grown under comparable conditions, with the result that he found crude protein content to be an inherent varietal characteristic, since he obtained an interannual correlation coefficient of 0.38 in a study of 40 pure lines of wheat. He also found a direct relationship between protein content and loaf volume within pure lines of a single variety.

Hayes et al. (*6*) report a general tendency for positive interannual correlations between the results obtained in different seasons when wheats of a diverse nature were grown under comparable conditions. The characters studied were protein content, loaf volume, flour percentage, and color and texture score of the cut loaf. All possible interrelationships of these characters were studied by correlation methods, without establishing many definite and consistent relationships. Protein content showed no consistent relation to loaf volume. There was some indication of a general tendency for positive correlations between loaf volume, color score of loaf, and texture score of loaf, but these relationships were not consistent under all conditions.

Waldron and Mangels (*13*) studied the relationship between protein content, water absorption of the flour, and volume of loaf in a series of wheats that were diverse in genetic origin but grown under conditions of uniform soil and treatment. Correlation of protein and water absorption and of water absorption and loaf volume was generally small and not significant. Protein and loaf volume gave fairly high correlations, the average for the nursery tests over a 4-year period being $r=0.441$.

## MATERIAL AND METHODS

The spring and winter wheats used in the milling and baking studies consisted of those strains or varieties that were being tested for disease resistance and desirable agronomic characters in the plant-breeding program of the Minnesota Agricultural Experiment Station during the years 1927–33. The varieties used in the tests were all semihard or hard red types; no soft wheats were included.

The samples used in the spring wheat rod-row tests were composites of grain from the border rows from the nursery plot trials made at the four State experiment stations located at University Farm, Waseca, Morris and Crookston. blended so as to secure comparable samples of

all varieties. Samples from the winter wheat rod-row trials were composites of grain from two stations, University Farm and Waseca. The samples obtained from the $\frac{1}{40}$-acre plots on each of the four stations were milled separately. These samples were not milled in replicate, as the grain available was insufficient, but baking tests were always replicated. Usually the bakings were duplicated, but occasionally as many as eight replicate bakings were made. The milling method used was that described by Markley (*9*), and the official baking procedure was that of the American Association of Cereal Chemists as reported by Blish (*3*) and Werner (*14*) with certain supplements that experience had shown to be desirable. Preliminary tests showed that the flour of the 1930 and 1931 crops, of both spring and winter wheat, was deficient in diastase. The use of 3 percent of high diastatic flour, as described by Markley and Bailey (*10*), was found to correct this deficiency and hence was used for the tests made with these crops. The characters from these milling and baking tests that were subjected to correlation analysis were test weight and protein content of the wheat, yield of straight grade flour, absorption, loaf volume, crumb color, crumb texture, and crumb grain.

To show the variation between the varieties grown and tested for milling and baking qualities, data for the more important characters of three varieties of spring wheat and of two varieties of winter wheat, together with the range of variability in each character for the varieties grown in each of the years at the four stations, are given in table 1.

The data given in table 1 show that for each of the characters there was considerable variation between the years, within a given variety, as well as a fairly wide range between the varieties grown each year. The varieties subjected to these milling and baking tests appeared to have desirable agronomic characteristics and disease resistance, and the data are those which would be obtained in any wheat-breeding improvement program.

The spring wheat varieties Marquis, Ceres, and Marquillo and the winter wheats Minturki and Minhardi were grown each year in the plots and rod-row nurseries during the entire period of the study. Most varieties or strains were tested for milling and baking qualities for at least 2 years before being discarded from the trials.

TABLE 1.—*Individual data on certain varieties and range of variability of all varieties for milling and baking quality of wheat grown at 4 Minnesota stations*

SPRING WHEAT 1/40-ACRE PLOTS

| Station | Year | Test weight | | | | Total flour | | | | Crude protein N×5.7 | | | | Loaf volume | | | | Color | | | | Texture | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Marquis | Ceres | Marquillo | Range | Marquis | Ceres | Marquillo | Range | Marquis | Ceres | Marquillo | Range | Marquis | Ceres | Marquillo | Range | Marquis | Ceres | Marquillo | Range | Marquis | Ceres | Marquillo | Range |
| | | *Lb.* | *Lb.* | *Lb.* | *Lb.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Cc* | *Cc* | *Cc* | *Cc* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* |
| University Farm | 1929 | 59 | 58 | 60 | 56–60 | 71 | 73 | 73 | 71–77 | 11 | 11 | 12 | 10–13 | 383 | 380 | 428 | 380–428 | 96 | 95 | 91 | 91–99 | 98 | 97 | 96 | 96–99 |
| | 1930 | 57 | 57 | 55 | 54–60 | 74 | 72 | 76 | 71–77 | 12 | 12 | 11 | 11–13 | 482 | 495 | 522 | 473–522 | 100 | 99 | 95 | 96–100 | 99 | 99 | 98 | 96–100 |
| | 1931 | 50 | 51 | 50 | 48–55 | 64 | 68 | 71 | 60–72 | 19 | 18 | 18 | 18–20 | 467 | 545 | 402 | 402–645 | 98 | 99 | 92 | 91–101 | 98 | 101 | 95 | 95–102 |
| | 1932 | 55 | 57 | 53 | 53–57 | 74 | 72 | 74 | 69–75 | 16 | 16 | 16 | 15–18 | 512 | 527 | 605 | 405–627 | 98 | 99 | 96 | 94–101 | 100 | 101 | 102 | 97–102 |
| | 1933 | 58 | 60 | 56 | 56–61 | 72 | 74 | 74 | 71–77 | 18 | 17 | 18 | 17–20 | 645 | 645 | 642 | 595–740 | 97 | 96 | 92 | 92–99 | 99 | 100 | 97 | 97–100 |
| Waseca | 1929 | 57 | 59 | 53 | 53–59 | 72 | 74 | 75 | 66–75 | 11 | 12 | 12 | 11–13 | 384 | 448 | 389 | 384–479 | 94 | 93 | 92 | 91–97 | 95 | 95 | 94 | 92–98 |
| | 1930 | 54 | 57 | 53 | 53–58 | 72 | 74 | 76 | 69–78 | 12 | 14 | 12 | 12–14 | 502 | 545 | 620 | 502–603 | 98 | 99 | 96 | 95–100 | 97 | 98 | 99 | 96–100 |
| | 1931 | 57 | 58 | 56 | 56–59 | 70 | 71 | 73 | 68–75 | 15 | 15 | 16 | 13–19 | 437 | 465 | 490 | 392–615 | 99 | 97 | 92 | 92–103 | 99 | 100 | 99 | 97–102 |
| | 1932 | 55 | 55 | 53 | 52–58 | 74 | 73 | 72 | 69–76 | 15 | 15 | 16 | 14–16 | 570 | 547 | 587 | 392–622 | 101 | 99 | 93 | 93–101 | 101 | 101 | 101 | 96–102 |
| | 1933 | 61 | 62 | 61 | 60–63 | 76 | 74 | 77 | 74–78 | 13 | 13 | 14 | 13–17 | 537 | 555 | 582 | 527–677 | 97 | 98 | 93 | 96–99 | 96 | 97 | 96 | 95–99 |
| Morris | 1929 | 56 | 56 | 56 | 56–61 | 73 | 74 | 76 | 69–78 | 12 | 12 | 13 | 11–14 | 413 | 428 | 463 | 413–489 | 95 | 94 | 91 | 91–99 | 97 | 98 | 96 | 96–99 |
| | 1930 | 57 | 57 | 54 | 53–60 | 73 | 73 | 76 | 73–80 | 13 | 14 | 13 | 11–14 | 502 | 577 | 567 | 492–618 | 99 | 98 | 93 | 93–100 | 99 | 94 | 99 | 94–100 |
| | 1931 | 56 | 57 | 54 | 54–57 | 72 | 70 | 73 | 66–81 | 16 | 16 | 16 | 16–18 | 455 | 502 | 485 | 405–555 | ---- | ---- | ---- | ---- | 100 | 100 | 100 | 99–102 |
| | 1932 | 54 | 56 | 52 | 52–58 | 73 | 73 | 73 | 70–75 | 16 | 16 | 17 | 15–17 | 500 | 577 | 505 | 462–600 | 100 | 99 | 93 | 93–100 | 98 | 101 | 99 | 96–101 |
| | 1933 | ---- | ---- | ---- | ---- | ---- | ---- | ---- | ---- | ---- | ---- | ---- | ---- | ---- | ---- | ---- | ---- | ---- | ---- | ---- | ---- | ---- | ---- | ---- | ---- |
| Crookston | 1929 | 52 | 58 | 54 | 50–60 | 71 | 71 | 75 | 68–79 | 15 | 13 | 16 | 12–16 | 478 | 431 | 473 | 415–499 | 96 | 96 | 93 | 93–105 | 98 | 98 | 97 | 93–105 |
| | 1930 | 59 | 59 | 57 | 57–60 | 76 | 76 | 77 | 74–80 | 11 | 11 | 12 | 11–14 | 502 | 503 | 530 | 493–592 | 99 | 99 | 95 | 95–101 | 98 | 98 | 96 | 95–100 |
| | 1931 | 56 | 59 | 58 | 55–60 | 72 | 78 | 75 | 67–78 | 15 | 15 | 16 | 14–17 | 485 | 517 | 552 | 417–560 | 100 | 99 | 95 | 93–100 | 100 | 100 | 101 | 99–101 |
| | 1932 | 55 | 55 | 52 | 52–57 | 70 | 73 | 73 | 70–74 | 16 | 16 | 17 | 15–17 | 557 | 570 | 445 | 445–605 | 101 | 100 | 92 | 92–101 | 99 | 99 | 97 | 97–100 |
| | 1933 | 62 | 62 | 62 | 54–63 | 78 | 77 | 72 | 72–80 | 13 | 13 | 13 | 13–16 | 452 | 550 | 532 | 452–645 | 97 | 99 | 93 | 93–100 | 96 | 99 | 96 | 95–100 |

SPRING WHEAT ROD ROWS

| | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| University Farm, Waseca, Morris, and Crookston. | 1929 | 55 | 56 | 53 | 52–59 | 75 | 78 | 77 | 72–80 | 13 | 13 | 14 | 13–16 | 423 | 466 | 463 | 393–505 | 96 | 99 | 92 | 91–103 | 97 | 99 | 94 | 94–101 |
| | 1930 | 56 | 57 | 54 | 53–59 | 72 | 76 | 75 | 72–79 | 15 | 14 | 15 | 14–16 | 570 | 603 | 566 | 468–730 | 98 | 98 | 94 | 92–100 | 97 | 99 | 96 | 93–101 |
| | 1931 | 54 | 55 | 53 | 53–57 | 72 | 68 | 71 | 65–77 | 17 | 17 | 18 | 16–18 | 503 | 570 | 420 | 418–670 | 101 | 100 | 94 | 93–101 | 100 | 100 | 98 | 97–101 |
| | 1932 | 54 | 56 | 52 | 52–57 | 72 | 75 | 73 | 72–77 | 15 | 16 | 16 | 15–17 | 562 | 625 | 512 | 472–597 | 100 | 102 | 92 | 92–101 | 101 | 102 | 100 | 100–102 |
| | 1933 | 59 | 60 | 58 | 57–61 | 76 | 75 | 77 | 75–78 | 16 | 16 | 17 | 13–17 | 640 | 607 | 650 | 485–582 | 98 | 100 | 93 | 93–102 | 99 | 99 | 97 | 93–100 |

WINTER WHEAT ROD ROWS

| Station | Year | Test weight | | | Total flour | | | Crude protein | | | Leaf volume | | | Color | | | Texture | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Minturki | Minhardi | Range | Minturki | Minhardi | Range | Minturki | Minhardi | Range | Minturki | Minhardi | Range | Minturki | Minhardi | Range | Minturki | Minhardi | Range |
| | | *Lb.* | *Lb.* | *Lb.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Cc* | *Cc* | *Cc* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* | *Pct.* |
| University Farm and Waseca [1] | 1927 | ------ | ------ | ------ | 71 | 71 | 68–71 | 13 | 14 | 12–15 | 455 | 456 | 408–464 | 98 | 98 | 97–99 | 97 | 98 | 97–99 |
| | 1929 | 54 | 55 | 54–60 | 77 | 72 | 72–79 | 10 | 10 | 10–11 | 425 | 440 | 385–486 | 89 | 92 | 89–97 | 94 | 94 | 89–100 |
| | 1930 | 58 | 57 | 57–60 | 73 | 72 | 72–77 | 11 | 11 | 11–12 | 488 | 383 | 438–455 | 93 | 95 | 92–99 | 98 | 96 | 96–100 |
| | 1931 | 56 | 56 | 55–58 | 74 | 73 | 69–77 | 15 | 15 | 11–15 | 380 | 312 | 365–447 | 92 | 92 | 91–97 | 94 | 92 | 92–98 |
| | 1932 | 54 | 55 | 53–57 | 67 | 71 | 67–79 | 14 | 14 | 13–15 | 477 | 455 | 445–567 | 92 | 93 | 93–99 | 97 | 96 | 96–100 |
| | 1933 | 62 | 60 | 60–62 | 75 | 75 | 74–78 | 13 | 13 | 13–15 | 485 | 502 | 485–502 | 96 | 93 | 92–100 | 97 | 94 | 94–101 |

[1] Composite sample.

## EXPERIMENTAL RESULTS

### INTERANNUAL CORRELATIONS

The interannual correlations for each succeeding pair of years and the average correlations for all years are given in tables 2, 3, and 4 for each of the three groups of samples, namely, the spring wheat rod rows, the winter wheat rod rows, and the spring wheat 1/10-acre plots. The significant correlations are in bold-faced type in these tables. It should be kept in mind that stem rust was not serious enough to affect appreciably the relative placings of the varieties during the years included in this study. Under rust-epidemic conditions susceptible varieties are so altered that any normal interannual correlation with a nonepidemic season is completely eliminated.

It may be seen in these tables that there is a moderate tendency for varieties to hold their relative ratings for test weight from year to year. The original records showed that certain varieties, such as Reward, tended to have a high test weight, while Hope was low in this character.

TABLE 2.—*Interannual correlation coefficients for test weight, total flour, crude protein, absorption, loaf volume, and color, texture, and grain scores of loaf obtained from winter wheats grown in rod rows at University Farm and Waseca, Minn., 1927–33*

| Years correlated | Comparisons | Interannual correlation coefficients | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Test weight | Total flour | Crude protein | Absorption | Characteristics of loaf | | | |
| | | | | | | Loaf volume | Color score | Texture score | Grain score |
| | *Number* | | | | | | | | |
| 1927, 1929 [1] | 9 | ..... | −0.54 | −0.23 | −0.12 | 0.47 | **0.81** | 0.66 | 0.19 |
| 1929, 1930 | 14 | 0.26 | **.78** | **.56** | −.47 | **.60** | **.55** | .29 | .15 |
| 1930, 1931 | 14 | .58 | .45 | .27 | .06 | .37 | **.88** | −.39 | .09 |
| 1931, 1932 | 14 | .30 | .28 | −.23 | **.55** | −.30 | **.74** | .48 | .12 |
| 1932, 1933 | 7 | −.27 | .03 | .65 | ..... | .63 | .58 | .40 | .64 |
| Average or total | 58 | [2].33 | **.37** | .20 | [3].03 | **.32** | **.75** | .25 | .19 |

[1] Crop failure in 1928.
[2] The number of comparisons in this case is 49.
[3] The number of comparisons in this case is 51.

TABLE 3.—*Interannual correlation coefficients for test weight, total flour, crude protein, absorption, loaf volume, and color, texture, and grain scores of loaf of spring wheat varieties grown in rod rows at University Farm, Waseca, Morris, and Crookston, Minn.*

| Years correlated | Comparisons | Interannual correlation coefficients | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Test weight | Total flour | Crude protein | Absorption | Characteristics of loaf | | | |
| | | | | | | Loaf volume | Color score | Texture score | Grain score |
| | *Number* | | | | | | | | |
| 1927, 1928 | 11 | ..... | 0.04 | −0.10 | −0.12 | **0.81** | 0.43 | 0.40 | −0.18 |
| 1928, 1929 | 31 | ..... | −.16 | −.10 | −.10 | **.38** | **.78** | .33 | .12 |
| 1929, 1930 | 25 | **0.58** | .27 | **.48** | **−.41** | **.43** | **.78** | .26 | −.29 |
| 1930, 1931 | 27 | **.55** | **.45** | −.01 | .27 | .46 | **.61** | **.69** | **−.48** |
| 1931, 1932 | 16 | .43 | .44 | .13 | −.21 | .15 | **.87** | .15 | .21 |
| 1932, 1933 [1] | 13 | .44 | .19 | .41 | −.35 | −.03 | **.80** | .28 | **.69** |
| Average or total | 123 | [2].52 | **.20** | .13 | −.13 | **.39** | **.74** | **.37** | −.06 |

[1] No data for Morris for 1933.
[2] Number of comparisons=81.

TABLE 4.—*Interannual correlation coefficients for test weight, total yield of flour, crude protein, absorption, loaf volume, and color, texture, and grain scores of loaf of the spring wheats grown in 1/10-acre plots*

| Years correlated | Interannual correlation coefficients [1] | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Test weight | | Total flour | | Crude protein | | Absorption | | Loaf volume | | Crumb color | | Crumb texture | | Crumb grain | |
| | *n* | *r* | *n* | *r* | *n* | *r* | *n* | *r* | *n* | *r* | *n* | *r* | *n* | *r* | *n* | *r* |
| 1929, 1930 | 56 | **0.55** | 56 | **0.60** | 55 | **0.70** | 56 | **0.31** | 56 | **0.35** | 52 | **0.58** | 56 | **0.42** | 56 | −0.01 |
| 1930, 1931 | 68 | .23 | 68 | **.50** | 68 | **.53** | 68 | .05 | 68 | **.41** | 51 | **.51** | 68 | .24 | 68 | −.09 |
| 1931, 1932 | 67 | **.55** | 67 | .16 | 67 | **.53** | 67 | .01 | 67 | **.45** | 52 | **.50** | 66 | .19 | 67 | **.42** |
| 1932, 1933 [2] | 36 | **.55** | 36 | .26 | 36 | .38 | 36 | .18 | 36 | .25 | 36 | **.64** | 36 | .20 | 36 | .13 |
| Average or total | 227 | **.46** | 227 | **.40** | 226 | **.54** | 227 | **.15** | 227 | **.39** | 191 | **.55** | 226 | **.27** | 227 | **.12** |

[1] *n* = Number of comparisons; *r* = correlation coefficient.
[2] No data at Morris in 1933.

There appears to be some basis for considering yield of total flour to be inherent, but the expression of this character is so obscured by random environmental effects that its usefulness is limited.

A similar situation holds with respect to crude protein content of the wheat. Although some varieties are consistently high or low in this character, many varieties appear to have a random type of variability.

In the group of baking scores there is one, crumb color, which appears rather definitely to be an inherent character because of the magnitude of its interannual correlations. This score is more nearly dependent upon one property of the wheat, namely, the carotinoid pigmentation, than are any of the other bread scores. In examining the individual interannual correlations of crumb color it should be kept in mind that in none of the years involved was there a serious epidemic of black stem rust that would have interfered with the expression of color. Interannual correlations for loaf volume were not large, although significant positive relationships were obtained for an average in each type of trial. There is little evidence of any inheritance of the properties of water absorption or of texture or grain of the loaf.

In a study of this type it must be kept in mind that there is considerable variation in both the response of the wheat plant to seasonal environmental factors and in the milling and baking procedure. When computing interannual correlations, therefore, the results of two highly variable tests are compared. It is not possible to grow a large number of varieties, so comparisons must be made between varieties grown in consecutive years. Higher correlations might have been obtained for some of the milling and baking characteristics if comparisons could have been made between averages of a considerable number of samples. It is possible and even probable that defects in the baking method used may have interfered with the proper expression of these characters. The possibility of this being the reason for the low interannual correlations is being investigated further at the Minnesota station.

## INTERSTATION CORRELATIONS

The interstation coefficients of correlation for each of the characters included in this study were first calculated for each of the individual

years and then averaged to give the values in table 5. Only the spring wheat data from the 1/10-acre plots could be used, because the rod-row samples consisted of composites from the different stations. These correlations indicate that, while each variety tends to react in the same manner when grown in different locations, differences in soil and climatic factors greatly influence the expression of milling and baking characteristics. This fact suggests the desirability of studying the reactions of wheat varieties under as many conditions as practicable. The variation existing between the ripening dates for different varieties probably is an important cause of the low order of these correlations. In some cases it may be desirable to investigate methods of culture for experimental plots whereby the dates of maturity could be made to coincide for varieties as diverse as Marquis and Reward, in order to obtain comparable data on inherent characters.

TABLE 5.—*Interstation correlation coefficients for quality characteristics of spring wheat varieties grown in 1/10-acre plots at four stations in Minnesota, 1929–33* [1]

| Stations correlated | Coefficients for average interstation correlation [2] | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Test weight | | Total flour | | Crude protein | | Absorption | | Loaf volume | | Color score [3] | | Texture score | | Grain score | |
| | *n* | *r* | *n* | *r* | *n* | *r* | *n* | *r* | *n* | *r* | *n* | *r* | *n* | *r* | *n* | *r* |
| University Farm and Waseca | 81 | **0.45** | 81 | 0.17 | 80 | **0.59** | 78 | **0.37** | 81 | **0.35** | 66 | **0.58** | 79 | **0.27** | 79 | **0.29** |
| University Farm and Morris | 66 | **.40** | 66 | .24 | 65 | **.65** | 67 | **.42** | 66 | **.38** | 34 | .22 | 66 | .20 | 66 | **.46** |
| University Farm and Crookston | 82 | **.27** | 82 | .01 | 80 | **.45** | 79 | **.33** | 82 | .23 | 67 | **.63** | 82 | .27 | 80 | **.37** |
| Waseca and Morris | 65 | **.68** | 65 | **.72** | 64 | **.60** | 62 | .24 | 65 | **.27** | 33 | .11 | 65 | **.28** | 65 | .20 |
| Waseca and Crookston | 81 | **.37** | 81 | **.32** | 80 | **.40** | 78 | .23 | 81 | .19 | 66 | **.58** | 79 | **.30** | 81 | **.36** |
| Morris and Crookston | 66 | **.41** | 66 | **.29** | 65 | **.47** | 63 | .12 | 66 | .09 | 34 | .34 | 66 | **.72** | 66 | **.48** |
| Total or average | 441 | **.44** | 441 | **.29** | 434 | **.52** | 427 | **.29** | 441 | **.29** | 300 | **.49** | 437 | **.35** | 437 | **.36** |

[1] No data at Morris in 1933.
[2] *n* = number of comparisons; *r* = correlation coefficient.
[3] No color data at any of stations in 1929.

## INTERRELATION BETWEEN CHARACTERS

The various coefficients of correlation between the characters for each of the three groups of samples are given in table 6. Some relations that have been found previously to be significant within varieties when grown under different environmental conditions do not appear to be of great importance when diverse varieties are included within the series and all varieties are grown under similar conditions. In this group are correlations of test weight with flour yield and protein content with crumb color. The small but significant positive correlations between protein content and loaf volume are in agreement, on the average, with the results of previous trials by other investigators.

The interlocking agreements between loaf volume, color, texture, and grain are as expected from long experience in test baking. This experience indicates that for a measure of color, texture, or grain the baking method should be so conducted as to yield bread of constant loaf volume, while for the determination of strength the volume should be pulled to a maximum. The results of these tests indicate some unsoundness in the underlying philosophy of baking-test methods now used that should be corrected as soon as methods can be developed.

TABLE 6.—*Interrelationships of the various milling and baking characteristics as expressed by the average correlation coefficients*

| Characters correlated | Coefficients of intercharacter correlations [1] | | | |
|---|---|---|---|---|
| | Rod rows | | 1/40-acre plots of spring wheat | |
| | Winter wheat [2] | Spring wheat [3] | | |
| | *r* | *r* | *r* | *n* |
| Total flour and test weight | **0.32** | 0.06 | **0.15** | 309 |
| Total flour and protein | .04 | −.07 | **.14** | 309 |
| Total flour and absorption | .22 | −.05 | .11 | 309 |
| Total flour and loaf volume | **.39** | −.06 | −.05 | 309 |
| Total flour and color | .11 | .03 | .11 | 276 |
| Total flour and texture | .04 | −**.20** | .02 | 309 |
| Total flour and grain | .12 | −.01 | −.06 | 307 |
| Protein and absorption | .15 | .08 | .08 | 309 |
| Protein and loaf volume | **.29** | **.16** | **.34** | 309 |
| Protein and color | **.43** | .15 | .12 | 287 |
| Protein and texture | **.25** | .13 | **.29** | 309 |
| Protein and grain | −.06 | **.16** | −.02 | 309 |
| Absorption and loaf volume | .14 | .05 | .11 | 309 |
| Absorption and color | −.17 | **.28** | **.16** | 287 |
| Absorption and texture | −.12 | **.24** | **.21** | 309 |
| Absorption and grain | −.12 | .15 | .04 | 307 |
| Loaf volume and color | **.32** | **.25** | **.22** | 287 |
| Loaf volume and texture | **.25** | **.23** | **.65** | 309 |
| Loaf volume and grain | **.60** | **.27** | .03 | 307 |
| Color and texture | **.50** | **.56** | **.63** | 287 |
| Color and grain | **.42** | **.35** | **.44** | 264 |
| Texture and grain | **.26** | **.42** | **.37** | 307 |

[1] *r*=Correlation coefficient; *n*=number of comparisons.
[2] Number of comparisons=88.
[3] Number of comparisons=188 except for total flour and test weight, where *n*=156.

## DISCUSSION

New varieties of wheat produced by the wheat breeder not only must have desirable agronomic characters and resistance to the more important plant diseases but they must also excel or equal in milling and baking qualities the best varieties grown commercially. These milling and baking qualities depend (1) on the inherent qualities of the varieties and (2) on the influence of environmental factors on these inherent qualities. At present there is no method available for the determination of the quality of new varieties during the early segregating generations. If such a method could be evolved it would greatly simplify the plant breeder's problem.

In the absence of such a method, however, it is necessary to mill and bake a large number of samples of the later generations when sufficient grain becomes available from the material grown under a normal range of environmental conditions. These milling and baking tests are made after the new strains have progressed to the rod-row plots. A composite sample of seed obtained from trials made in different localities within the State is used. The data obtained from such tests are used to aid in selecting the more promising wheats and in discarding the less desirable ones. Later, as more seed becomes available, varieties as grown in each locality may be milled and baked.

The most striking feature of the milling and baking data on these wheats was the relatively low magnitude of the observed interannual coefficients of correlation for most characters. The outstanding exceptions to this low order of correlation were crumb-color scores. It would appear that the relative placing of wheat varieties for this character was less affected by environmental factors than was

the placing for any other character. However, in the placing for crumb color other factors tended to interfere with this relation. To some extent, as indicated by the numerous significant correlations, the crumb color was partly a function of the loaf volume and of the nature of the crumb of the cut loaf. From a plant-breeding standpoint, therefore, it would seem necessary to make tests for color of flour in the early stages, and methods are available for making these determinations.

The milling yield as expressed in percentage of total flour secured from the wheat tended to be independent of all the factors that affect the baking results. The interannual average correlations for total flour were usually significant and positive but of a low order. The same was true of the interstation correlations, with the exception of the high correlation of $r=0.72$ for Morris and Waseca. It has been shown by many workers, as well as by the accumulated knowledge of practical millers, that the milling yield is largely a function of the test weight of the wheat, although correlation coefficients of low order were obtained in this study. The test weight of the wheat has been shown repeatedly to be reduced by such factors as moisture deficiency in the soil during the ripening period, hot and desiccating atmospheric conditions, frosts, and attacks of diseases such as rusts and root rots.

During the years of these trials the test weights were frequently adversely affected by one or more of these factors with the exception of frost. The varieties used had different dates of ripening, there being a range of over a week between the earliest and the latest varieties. Under these conditions it is not surprising that there were not high interannual and interstation correlations of milling yield. The milling yield should never be considered without keeping in mind at the same time the test weight of the wheat and the kernel texture.

Crude protein content is often rather closely correlated with loaf volume when commercial samples are compared. In previous studies with wheats of diverse nature, grown under similar environmental conditions, Hayes et al. (*6*) found little evidence of consistent correlation between loaf volume and crude protein. In the present studies, carried over many years, there was opportunity to draw more accurate conclusions.

Interannual correlations for crude protein content and loaf volume for rod rows of winter wheat were 0.20 and 0.32, respectively, the latter reaching the 5-percent point; for spring wheat rod rows, 0.13 and 0.39, respectively, the latter reaching the 5-percent point; in the $\frac{1}{40}$-acre plots of spring wheat both correlation coefficients were significant, being 0.54 and 0.39 respectively.

In interstation correlations during the same years, the coefficients for crude protein exceeded the 5-percent point in each case and ranged from 0.40 to 0.65. With loaf volume all six correlations were positive, three reaching the 5-percent point. These facts lead to the conclusion that inheritance is of considerable importance for both crude protein and loaf volume but that environmental conditions tend strongly to modify the results of individual comparisons.

When data of all tests are combined, giving $n$ values of 88, 188, and 309, the correlations between crude protein and loaf volume are 0.29, 0.16, and 0.34, respectively, which certainly are of little selection value although they do show positive relationship.

The baking test is an extremely complicated biochemical and biophysical process. Because of its complexity and sensitivity to environmental influence, it is fully as difficult to control for scientific purposes as is the growing of the varieties of wheat in truly comparable tests by the agronomist. Test-baking procedures may be classified in two fundamentally different categories. One includes those tests that subject all samples to a more or less rigid technique and set of conditions, the other includes those that tend to give each sample its optimum treatment. At present there is no evidence that conclusively proves one of these categories to be superior to the other for wheat-variety testing. The method used in the studies here reported was the rigid procedure for all varieties. Thus the variations observed could be said to be functions of the variety or station or year rather than of the method. These variations might or might not have been observed if some other baking technique had been employed. The milling and baking tests for the years 1927 and 1928 were conducted by one technician, and all samples from 1929 to 1933, inclusive, were milled and baked by a second technician. In this way personal variability was held close to a minimum.

The various scores of the bread tended to be correlated, but most coefficients were rather small. In the winter wheats the correlation of loaf volume and crumb grain was $r = 0.60$, while in the spring wheats from the $\frac{1}{40}$-acre plots it was very low, being $r = 0.03$. In the winter wheats the grain scores closely followed the loaf volumes, but the spring wheat loaves exhibited a wide range in grain scores at each loaf-volume level. Some varieties, such as Marquillo, tended to give a coarse, open grain regardless of volume. Certain other varieties of questionable gluten strength gave very poor grain with a large volume. Other varieties, such as Marquis, gave uniformly good grain at widely varying levels of loaf volume. Loaf volume and crumb texture were found to be correlated; this was especially noticeable on some of the spring wheat flours from the rod-row series in which the volume was large and the texture very soft and silky. Crumb color was correlated with texture and grain. This was due to shadows cast by the cell walls, making coarse-grained bread darker in color than the fine, even-grained type. This relation did not hold in the case of extremely tight-grained loaves, because the thickness of the cell walls gave undue yellowness to the appearance of the slice.

## SUMMARY

Milling and baking tests were made on varieties of wheat grown as a part of the wheat-breeding program during the years 1927–33, in the rod-row and $\frac{1}{40}$-acre varietal trials of the Minnesota Agricultural Experiment Station.

Correlation analysis was used to determine interannual, interstation, and intercharacter relationships for the characters of test weight, wheat protein, milling yield of straight grade flour, water absorption of the dough, loaf volume and color, and texture and grain of the cut crumb of the loaf.

The magnitude of the interannual correlations tended to be rather low with the exception of crumb color, which appeared to be more independent of interfering environmental variables than did the other factors.

Interstation correlations tended to be significant but of a low order of magnitude, indicating a need for further study of the environmental factors that affect milling and baking quality and the desirability of developing practical methods of handling experimental plots so that all varieties will mature at the same time instead of with a spread of a week or more as at present.

Intercharacter correlations indicate a close relation between loaf volume and color, texture, and grain. The relation between test weight, protein content, and milling yield was not apparent when varieties of diverse origin were compared.

Better methods for determining the baking quality of wheat varieties are very urgently needed and should be based upon sound biological and physical studies.

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# CORRELATION OF BODY MEASUREMENTS OF SLAUGHTER STEERS WITH RATE AND EFFICIENCY OF GAIN AND WITH CERTAIN CARCASS CHARACTERISTICS [1]

By W. H. BLACK, *senior animal husbandman*, BRADFORD KNAPP, JR., *associate animal husbandman*, and A. C. COOK, *associate animal husbandman, Animal Husbandry Division, Bureau of Animal Industry, United States Department of Agriculture* [2]

## INTRODUCTION

As a part of record-of-performance work at the Agricultural Research Center, Beltsville, Md., the cattle used in such work were measured at the time of slaughter to determine whether any relationship existed between body measurements and various production factors and meat characters. The record-of-performance procedure necessitated that all the animals be of approximately the same weight (*1, 10*).[3] For this reason, the data are for a nearly weight-constant population. The variation in slaughter weight was about ±20 pounds from a mean of 900 pounds live weight. The results of the correlation study are reported herein.

## REVIEW OF LITERATURE

In a study of type in beef calves, Hultz (*5*) showed that the most important measurements for the determination of low setness are depth of chest, paunch circumference, and height at withers. In a study made at time of slaughter, Hultz failed to obtain a significant correlation between any of the body measurements of the calves and their type. The highest correlation he obtained was between the ratio of chest depth to height at withers and type. This correlation was too low to be significant.

In a study of type in 2-year-old steers, Hultz and Wheeler (*6*) showed that a steer has the appearance of being low-set when the proportions of his chest depth, heart girth, and paunch girth to height are great. In other words, a low-set steer has a large heart girth, is deep of chest, and has a large paunch girth in proportion to the height at withers.

Lush (*8*) obtained a correlation of 0.563 between estimated fatness and a ratio of heart girth to height at withers of the steer. This is the highest correlation with estimated fatness obtained. The ratio of loin width to heart girth gave a correlation of 0.076. He concluded that ratios involving chest width have higher correlations, larger average changes due to fattening, and larger standard deviations of the changes than ratios involving loin width. This finding seems to indicate that width of chest is more closely related to fatness than width of loin but was not measured so accurately as width of loin.

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[2] Acknowledgment is made to O. G. Hankins and R. L. Hiner, of the Animal Husbandry Division, for making the meat studies and to L. B. Burk, A. T. Edinger, and M. T. Foster, of the Bureau of Agricultural Economics, for cooperation in grading the slaughter cattle.
[3] Reference is made by number (italic) to Literature Cited, p. 472.

In a study of the relation of body shape of feeder steers to rate of gain, to dressing percentage, and to value of dressed carcass, Lush (*9*) showed that for high dressing percentages and dressed-carcass values, the most important measurements are a large heart girth in connection with a shallow chest, a wide loin, and large flank girth, a large initial weight, small paunch girth, head narrow at the eyes, and a short height over hips. Maximum gains, Lush concluded, are associated with a long body, tall at the withers, with a large paunch girth but small flank girth and narrow at the loin—a big skeleton but poor in flesh.

Knapp and Cook (*7*) demonstrated that between beef and dual-purpose Shorthorns certain differences exist in body measurements and in ratios of body measurements. According to their data, with steers slaughtered at 900 pounds weight the animals with the lowest height at withers are of the better beef type. In a study of the ratio of height at withers to heart girth they showed that there is a significant difference between beef and dual-purpose cattle.

## MATERIAL AND METHODS

The 50 animals used in this study were record-of-performance steers of beef, dual-purpose, and dairy breeding. They were fed individually corn, oats, wheat bran, and linseed meal before weaning and corn and alfalfa hay after weaning. All animals were weaned at 252 days of age. As already stated, the population studied was nearly weight constant, the steers being slaughtered at as nearly 900 pounds live weight as possible.

A committee consisting of three men familiar with the standard market grades of steers, as adopted by the United States Department of Agriculture, graded the slaughter steers. Figure 1 shows the position of all the measurements taken on an animal.

Correlations were obtained between the various body measurements, or ratios of body measurements (shown in table 1), and efficiency of gain, average daily gain, dressing percentage, percentage of fat in carcass, percentage of total edible meat in carcass, and slaughter grade. The correlations were computed according to the methods of Wallace and Snedecor (*11*). Yapp's index is computed as outlined in his paper (*12*). This index takes into consideration height, length, and weight of the animal. No standard error was computed, but, according to Fisher (*4*), for a $P$ of 0.05 based on a sample of 50, the correlation, to be significant, must be higher than 0.273, and for a $P$ of less than 0.01 the correlation must be higher than 0.354. Thus, in the following results, correlations higher than 0.354 are considered significant, whereas those between 0.273 and 0.354 are considered of questionable significance.

## RESULTS

In table 1 are shown the positive and negative correlations between the various body measurements and factors of beef production.

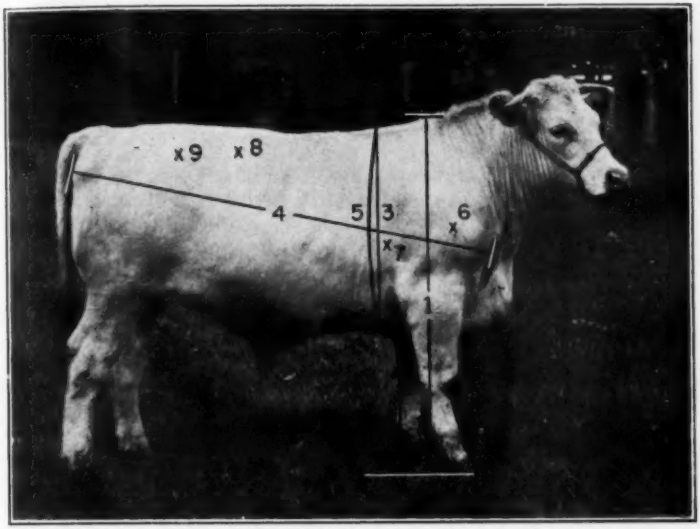


FIGURE 1.—Location of measurements studied: 1, Height at withers; 2, height of floor of chest; 3, depth of chest; 4, length of body from pinbone to shoulder point; 5, heart girth; 6, width of shoulder; 7, width of chest; 8, width of loin; and 9, width of hips. (× indicates measurements taken through body.)

TABLE 1.—*Correlations of body measurements and ratios of body measurements with the factors indicated, in record-of-performance steers*

| Body measurements | Efficiency of gain | Average daily gain | Dressing percentage | Percentage of fat in carcass | Percentage of total edible meat | Slaughter grade |
|---|---|---|---|---|---|---|
| Height at withers | −0.3667 | −0.1907 | −0.5011 | −0.7989 | −0.8296 | −0.8293 |
| Height of floor of chest | −.2909 | −.1252 | −.4602 | −.6974 | −.6762 | −.7105 |
| Depth of chest | −.2425 | −.1871 | −.3857 | −.4613 | −.5467 | −.5290 |
| Length of body | −.4335 | −.3224 | −.4875 | −.6347 | −.7116 | −.7447 |
| Heart girth | +.0721 | −.0542 | +.1283 | +.2969 | +.2240 | +.3908 |
| Width of shoulder | +.4504 | +.4212 | +.3800 | +.4113 | +.4447 | +.6144 |
| Width of chest | +.3390 | +.2929 | +.5019 | +.5844 | +.5769 | +.6605 |
| Width of loin | −.0517 | −.0527 | −.1104 | −.1557 | −.0973 | −.0572 |
| Width of hips | −.0910 | −.2002 | +.1904 | +.2509 | +.2094 | +.3585 |
| Ratio of heart girth to height | +.3226 | +.1216 | +.5356 | +.7611 | +.7600 | +.8252 |
| Yapp's index | −.4430 | −.2850 | −.5659 | −.7632 | −.7934 | −.8593 |
| Ratio of body weight to height | +.4407 | +.3323 | +.5320 | +.7537 | +.7668 | +.8361 |
| Heart girth × 100 / Height × length | +.4063 | +.2301 | +.5631 | +.7736 | +.8072 | +.8713 |
| Ratio of width of chest to height at withers | +.4042 | +.2900 | +.6144 | +.7362 | +.7498 | +.8145 |
| Slaughter grade | +.4962 | +.3541 | +.6431 | +.8201 | +.8325 | |

## CORRELATIONS WITH BODY MEASUREMENTS

Height at withers is, strictly speaking, a skeletal measurement and shows a negative correlation with all the factors studied. The correlation between height at withers and efficiency of gain is significantly negative. The taller, rangier type of animal, therefore, has a slight tendency to put on gains less economically than the shorter, blockier type. However, there was no significant correlation between height at withers and rapidity of gain. According to the results obtained, the shorter type steers have the higher dressing percentage; the rangier,

taller animals are lower in this respect. This correlation is significant. Height at withers was highly correlated negatively with percentages of fat and edible meat in the carcass. The taller type animals, therefore, have less fat and less total edible meat than the lower, blockier type. There is a very high negative correlation between height at withers and slaughter grade.

Length of leg, as shown by height of floor of chest, has a negative correlation with the production factors considered. The correlations are not so high throughout as those involving height at withers, but they are in about the same order. The correlation between height of floor of chest and efficiency of gain is of questionable significance, whereas that between height of floor of chest and average daily gain is not significant.

Depth of chest appears to be a skeletal measurement in that, like other skeletal measurements, the correlations are all negative. Again the correlations are slightly lower than those involving height at withers. From the three measurements so far discussed, it can be concluded that with weight constant, the shorter in height, shorter legged, shallower type of animal is higher in efficiency of feed utilization and has more fat, more edible meat, and less bone in the carcass than the taller, longer legged, deeper bodied animal. This is in agreement with the findings of Lush (*9*).

Length of body, as measured from pinbone to shoulder point, shows higher correlations with efficiency of gain and with rapidity of gain than does height at withers but lower correlations with dressing percentage, percentage of fat, and percentage of edible meat. The correlation between height at withers and length of body is 0.6957. The fact that the coefficient of alienation equals the coefficient of correlation does not necessarily indicate that an animal short in height is short in body. The actual length of body shows considerable variation from the estimated length derived from the actual height at withers, computed by the estimating equation from the correlation of 0.6957. In other studies made by the writers, length of body had a much higher correlation with efficiency of gain than did height at withers. In the present study the difference is not significant. It may be concluded, however, that length of body is associated more closely with efficiency of gain than is height at withers.

As shown by table 1, negative correlations were obtained between all the skeletal measurements and the quality of the end product, as judged by the quantity of meat or fat or the slaughter grade of the animal. This result is to be expected in a nearly weight-constant population.

Heart girth shows only two correlations of even questionable significance—those involving percentage of edible meat and slaughter grade. With a weight-constant population, it is not expected that there would be any correlation between heart girth and the remaining four factors. Heart girth has been used to determine weight of animal, and the relationship between these two factors is very close. The positive correlation between heart girth and slaughter grade shows that condition of fleshing plays a part in size of heart girth for a given weight.

Width of shoulder and width of chest show positive relationships with all the factors studied. The correlations involving width of

shoulder are consistently higher for efficiency of gain and lower for the characteristics of the slaughter animal than the correlations involving width of chest.

Width of loin is not correlated with any of the factors. The correlations are consistently negative but none may be considered significant. This finding is contrary to that of Lush (*8*), who shows that width of loin makes next to the largest change with increasing fatness. Lush's data were not used for a weight-constant population.

Width of hips shows low insignificant negative correlations with efficiency and rapidity of gain and low positive correlations with slaughter grade, percentage of fat, percentage of edible meat, and dressing percentage of the animals. The only correlation that may be considered significant is between width of hips and slaughter grade.

### CORRELATIONS WITH RATIOS OF BODY MEASUREMENTS

The correlations of ratios of body measurements with production factors are rather high when compared with the results obtained by Lush (*8*) and by Hultz (*5*, *6*). This lack of agreement may be caused by the fact that the population studied by the present authors was a weight-constant group, whereas the populations studied by Lush and Hultz were not.

The ratio of heart girth to height at withers has a significant correlation with dressing percentage, percentage of edible meat, percentage of fat, and slaughter grade but not with either efficiency of gain or rapidity of gain. The correlation of 0.76 with percentage of edible meat in the carcass shows that this ratio may be used as a method of predicting percentage of total edible meat. A well-finished steer, therefore, should be less tall for a given circumference of chest than a poorly finished steer.

Since there were certain slight deviations in weights of the animals at time of slaughter, a ratio of weight to height at withers was computed. The correlations show that it is a better measure of slaughter grade, percentage of edible meat, and efficiency of gain than is the ratio of heart girth to height at withers. These correlations are about the same as those obtained with height at withers alone, except that one group is positive and the other negative.

Yapp's index, although negative, shows in respect to efficiency and carcass characteristics, with the exception of dressing percentage, the highest correlations of the group of ratios. Only one of the correlations, average daily gain, is of doubtful significance; the others are highly significant. This index may be used to estimate percentage of fat and percentage of total edible meat but is not so efficient as the judgment of an experienced grader. Percentage of fat may be estimated from slaughter grade with 9 percent less error, and percentage of total edible meat with 6 percent less error, than from Yapp's index. The fact that weight is constant may account for higher correlations than Yapp has shown. The difference in correlations between Yapp's index and the weight-height ratio is very small, and because of the number of measurements required in the Yapp index it is not believed that it is a much better measure.

The ratio $\frac{\text{heart girth} \times 100}{\text{height} \times \text{length}}$, suggested by Duerst (*3*), is similar to

the Yapp index. The correlations are higher than those shown for the ratio of heart girth to height at withers, and in most instances are superior to those obtained by the weight-height ratio. The ratio $\frac{\text{heart girth} \times 100}{\text{height} \times \text{length}}$ shows a higher correlation with slaughter grade, percentage of fat, and percentage of edible meat than any of the other ratios. The correlation with slaughter grade of 0.8713 is high enough to be of use in determining the dressing percentage, percentage of fat, and percentage of edible meat of an animal. Likewise, the high correlation with percentage of total edible meat makes possible the use of this ratio to estimate percentage of total edible meat. However, it is not so easy to use as the ratio of body weight to height at withers, and the difference is not great enough to warrant the time required to measure anything except height at withers.

The ratio of width of chest to height at withers is in fair agreement with the other ratios. As a whole, this ratio does not show as high correlations as the other ratios. The correlations with efficiency of gain, average daily gain, and dressing percentage are higher than those obtained by the use of the ratio of heart girth to height at withers, whereas the correlations of percentage of fat, percentage of edible meat, and slaughter grade are lower than those obtained by this ratio.

Slaughter grade shows throughout higher correlations than any of the ratios. That visual observation should be superior to measurements or ratios of measurements seems reasonable since measurements cannot show exactly the symmetry and proportions that should exist in a good beef-type animal. All the correlations obtained through the use of slaughter grade are significant. The correlation of 0.8325 with percentage of edible meat in the carcass shows that selections are being made of animals with low percentage of bone. Taken as a whole, the correlations indicate that committee judgment is a more accurate estimate of the worth of an animal than any ratios of body measurements. Lush (*8*) concludes that measurements should be regarded as supplementary and confirmative of the inferences drawn from weight and appearance rather than as a substitute for the information gained from the study of the weights alone. The authors have likewise found it to be true in regard to slaughter grade of animal; measurements can well be a part of such studies but should not be substituted for slaughter grade of the animal.

The authors found that when weight of the animals is kept constant there is a much higher relationship between body measurements and ratios of measurements and various production factors than either Lush or Hultz found in their studies. A comparison of the ratios and their correlations shows that Yapp's index, in general, gives the highest correlations with efficiency of gain and with the carcass characteristics studied. The weight-height ratio gives almost as high correlations and for all practical purposes they may be considered the same. The heart girth-height ratio on an average gives the poorest correlations in the group of ratios, although the correlation with slaughter grade is high.

To make use of these ratios a study must be made of changes occurring in the ratios during the life of an animal; in other words, changes in the ratios due to increasing fatness, weight, and age. The ratio of weight to height, for instance, changes gradually from about

1.2: 1 at birth to 7.5: 1 at 15 months of age, as found by the authors in a study with Shorthorn steers, the number in the various groups ranging from 6 to 23. The results agree in general with those of Brody and his coworkers (*2*), who used Hereford and Shorthorn steers (fig. 2). These findings show that if this ratio is to be of use in a random-weight population, an age correction factor must be employed. The important point is that the ratio between any one of the skeletal measurements and weight changes with age as well as with fatness.

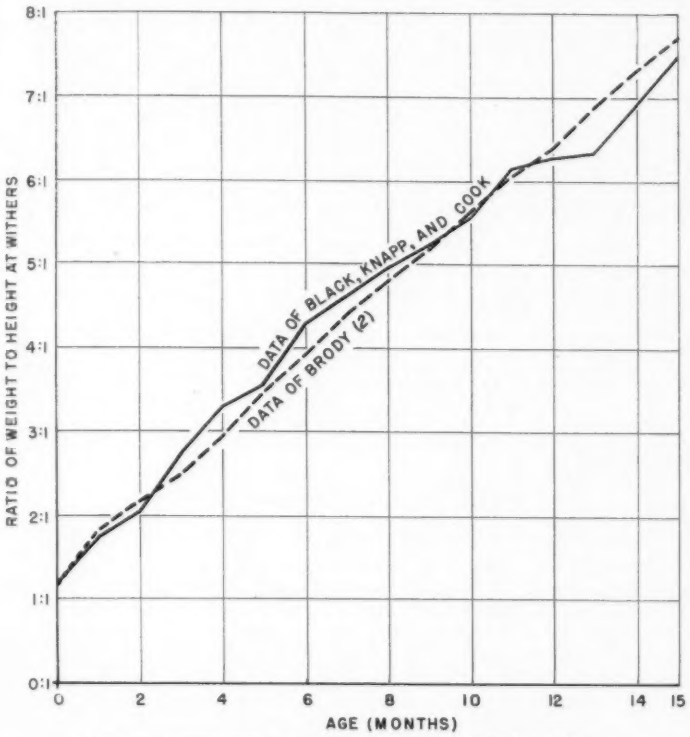


FIGURE 2.—Effect of age of steers on ratio of weight to height at withers.

The recent trends in beef type have been to produce the most meat with the least skeletal growth. Such a trend should not go to the extreme in small skeletal growth.

## SUMMARY

A correlation study was made of the body measurements, in relation to efficiency of gain, average daily gain, dressing percentage, percentage of fat in carcass, percentage of total edible meat, and slaughter grade, of 50 head of record-of-performance steers slaughtered at the Agricultural Research Center, Beltsville, Md. They were of beef, dual purpose, and dairy breeding. All animals were slaughtered at approximately 900 pounds of live weight.

Correlations indicate that height at withers (with weight nearly constant) is one of the best measurements of performance, although length of body had a higher correlation with efficiency of gain and average daily gain than did height at withers.

Of the ratios of measurement studied, a ratio of weight to height at withers gave a higher correlation with performance factors than any other ratio for the number of measurements taken. Yapp's index, which takes into consideration the height, weight, and length of the animal, gives in general the highest correlations. However, the differences between them and the correlations obtained by the use of the weight-height index are not sufficiently great to justify taking the large number of measurements required in the use of Yapp's index.

Slaughter grade was found to be a better measure of beef type than any ratios of measurements. Therefore, measurements should not replace, but should supplement, reliable slaughter grades.

If any ratio is used, corrections will have to be made for differences in fatness, weight, and age of the animal, for these ratios do not remain constant for any one individual during the entire course of its life.

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